Journal of the Fisheries Research Board of Canada

Journal de l'office des recherches sur les pêcheries du Canada

Volume 35, No. 3, March 1978

Volume 35, nº 3, mars 1978

Fisheries and Environment Canada
Fisheries and Marine Service

Pêches et Environnement Canada
Service des pêches et de la mer

Journal of the Fisheries Research Board of Canada

Journal de l'office des recherches sur les pêcheries du Canada

Fisheries and Environment Canada
Fisheries and Marine Service
Scientific Information and Publications Branch
Ottawa K1A 0E6

Pêches et Environnement Canada
Service des pêches et de la mer
Direction de l'information et des publications scientifiques

Volume 35, No. 3, March 1978

Volume 35, nº 3, mars 1978

The *Journal of the Fisheries Research Board of Canada* has been published continuously since 1901, previously as *Contributions to Canadian Biology* 1901–25, *Contributions to Canadian Biology and Fisheries* 1926–34, and *Journal of the Biological Board of Canada*, 1934–37.

Editorial policy — The *Journal* publishes original research articles and notes, critical reviews, essays of opinion or hypothesis, letters, and book reviews in the broad field of fisheries management and technology, ocean science, and aquatic environments relevant to Canada. Submissions in English or French are accepted without limitations as to origin, but must not have been published or copyrighted and must not be published elsewhere except in abstract form or by written consent of the Editor. The *Journal* accepts no responsibility for statements made by contributors. The use of proprietary names does not imply endorsement of the product or company. Guides for authors and typists appear in the first issue of each volume and are available free from the *Journal*.

A charge of $44 per page is made for manuscripts published. When submitting a manuscript, an author must state that the charge will be accepted.

Subscriptions — The *Journal* is issued monthly to form annual volumes of twelve numbers. Subscription rates are: Canada, $40 per year; other countries, $48. Single issues are $4 and $4.80, respectively. Orders must be sent directly to Supply and Services Canada, Ottawa, Canada, K1A 0S9, and payment made in Canadian funds to "The Receiver General for Canada."

Microfilm — Issues from 1934 through the current volume can be purchased on 16 or 35 mm microfilm. Photocopies of individual articles or issues can be purchased. Address orders to Xerox University Microfilms, 300 North Zeeb Road, Ann Arbor, Michigan 48106, USA.

Publié depuis 1901, le *Journal de l'office des recherches sur les pêcheries du Canada* a paru sous plusieurs titres: *Contributions to Canadian Biology*, 1901–25, *Contributions to Canadian Biology and Fisheries*, 1926–34, et *Journal of the Biological Board of Canada*, 1934–37.

Politique de publication — Le *Journal* publie des articles de recherches, ainsi que des notes, critiques, exposés d'opinions ou d'hypothèses, lettres et recensions concernant le vaste domaine de la gestion des pêches et de la technologie, des sciences de la mer et des milieux aquatiques au Canada. Toutes contributions en français ou en anglais sont acceptées sans restriction quant à la provenance, mais elles ne doivent pas avoir été produites ni avoir fait l'objet d'un copyright et ne doivent pas être publiées nulle part ailleurs sauf sous forme abrégée ou avec le consentement écrit du directeur. Le *Journal* décline toute responsabilité pour ce qui est des affirmations des collaborateurs. L'utilisation de noms de marque de commerce ne signifie aucunement une sanction du produit en question ou de la compagnie qui le fabrique. Le guides des auteurs et le guide des dactylos paraissent dans le premier numéro de chaque volume et sont disponibles gratuitement du *Journal*.

Les frais de publication sont de $44 la page. Quant un auteur présente un texte, il doit préciser que ces frais seront acceptés.

Abonnement — Le *Journal* paraît tous les mois, formant ainsi un volume de 12 numéros par année. Les frais d'abonnement annuel sont de $40 pour le Canada et de $48 pour les autres pays. Chaque numéro coûte $4 au Canada et $4.80 à l'étranger. Prière d'adresser directement les commandes à Approvisionnements et Services Canada, Ottawa (Ontario), Canada K1A 0S9; les paiements doivent être faits en devises canadiennes, à l'ordre du Receveur général du Canada.

Microfilms — On peut acheter sur microfilms 16 ou 35 mm tous les numéros publiés depuis 1934. Des photocopies d'articles ou de numéros individuels sont aussi en vente. Prière d'adresser les commandes à Xerox University Microfilms, 300 North Zeeb Road, Ann Arbor, Michigan 48106, E.-U.

Editor and Director of Scientific Information/ Rédacteur et Directeur de l'information scientifique — J. C. STEVENSON, PH.D.

Deputy Editor/Sous-rédacteur — J. WATSON, PH.D.

Assistant Editors/Rédacteurs adjoints — D. G. COOK, PH.D./LORRAINE C. SMITH, PH.D.

Production-Documentation — J. CAMP/G. NEVILLE/PAULA IRVING/C. T. CARMODY

French Abstracts/Résumés français — Y. JEAN, PH.D.

Book Review Editor/ Rédacteur des comptes rendus — D. P. SCOTT, PH.D.

Journal of the Fisheries Research Board of Canada

Volume 35, No. 3, March 1978

Journal de l'Office des recherches sur les pêcheries du Canada

Volume 35, nº 3, mars 1978

A Simple Fish-Population Model Including Environmental Influence, for Two Western Atlantic Shelf Stocks[1]

R. H. LOUCKS

R. H. Loucks Oceanology Limited, Halifax, N.S. B3M 1L3

AND W. H. SUTCLIFFE JR.

Department of Fisheries and the Environment, Fisheries and Marine Service, Marine Ecology Laboratory, Bedford Institute of Oceanography, Dartmouth, N.S. B2Y 4A2

LOUCKS, R. H., AND W. H. SUTCLIFFE JR. 1978. A simple fish-population model including environmental influence, for two western Atlantic shelf stocks. J. Fish. Res. Board Can. 35: 279–285.

For several Scotian Shelf and Gulf of Maine stocks, correlations have been observed between ocean temperatures, subsequent fish catches, and fishing effort. We consider a simple fish-population model relating these elements. We suggest that variation in ocean climate triggers corresponding fluctuations in fish stock–recruitment and subsequent abundance and catch. Two pathways between abundance and catch are recognized: (1) catch is simply proportional to abundance (direct influence); and (2) in some cases at least, fishermen traditionally have sensed the abundance of a stock and adjusted their fishing effort accordingly; therefore, in periods of less favorable climate for a stock, catch would diminish indirectly because of reduced or "responsive" effort. In such cases, where the fishermen act to stabilize the stock, fishing effort and fish catch are correlated with ocean climate. In any case, ocean climate and "responsive" effort merit consideration as potentially significant factors in population models of these stocks.

Key words: fish-population model, effort, recruitment, abundance, cod, yellowtail flounder

LOUCKS, R. H., AND W. H. SUTCLIFFE JR. 1978. A simple fish-population model including environmental influence, for two western Atlantic shelf stocks. J. Fish. Res. Board Can. 35: 279–285.

Nous avons observé sur plusieurs stocks du plateau de la Nouvelle-Ecosse et du golfe du Maine, des corrélations entre les températures de l'océan, les prises de poissons et l'effort de pêche. Nous examinons un modèle de population simple établissant une relation entre ces éléments. D'après les résultats, la variation dans le climat océanique déclencherait une variation correspondante dans le recrutement des stocks de poissons, l'abondance et les prises subséquentes. Nous reconnaissons deux voies reliant la prise à l'abondance : (1) la

[1]Bedford Institute of Oceanography Contribution.

Printed in Canada (J4915)
Imprimé au Canada (J4915)

prise est simplement proportionnelle à l'abondance; et (2) dans certains cas du moins, les pêcheurs ont traditionnellement pressenti le niveau d'abondance d'un stock et réglé leur effort de pêche en conséquence; en périodes de climat défavorable pour un stock, la prise devrait donc diminuer, indirectement par suite d'un effort réduit ou « flexible ». Dans de tels cas, quand les pêcheurs tâchent de stabiliser le stock, l'effort de pêche et la prise sont reliés au climat océanique. De toute façon, le climat océanique et l'effort « flexible » méritent considération : ils peuvent être des facteurs importants dans les modèles de population de ces stocks.

Received July 11, 1977
Accepted November 24, 1977

Reçu le 11 juillet 1977
Accepté le 24 novembre 1977

THE influence of environmental fluctuations on fisheries has been our concern for some time. Sutcliffe (1972, 1973) has drawn attention to correlations between St. Lawrence River discharges and Gulf of St. Lawrence fish catches a few years subsequently, and more recently we have studied the correlations between some western Atlantic shelf fish catch records and sea temperatures. In the course of this work we offered evidence for an oceanographic pathway along which environmental signals appeared to propagate southwestward along the shelf at ocean drift speeds from Cabot Strait to the Gulf of Maine with concomitant implications for juvenile fish survival (Sutcliffe et al. 1976, 1977).

The latter approach included empirical modeling using regression techniques to establish simple equations for fish catch based on local sea temperatures and then on temperatures and fishing effort.

In the present paper, we describe a simple fish-population model that includes the influence of environmental fluctuations. We have striven for a conceptually improved representation including the processes of recruitment and mortality and the influence of environmental fluctuations on the former. This model is cast in terms of numerical abundance rather than biomass. Self-limiting effects are expressed in the density-dependent mortality of the Ricker recruitment curve. Alternatively, one could utilize the density dependence of the logistic model as Schaefer (1954) has done.

The Model

The model expresses change of abundance as the net of recruitment and mortality:

$$(1)\quad \frac{\Delta N_t}{\Delta t} = \alpha N_{t-l}\, e^{-\beta N_{t-l}} \left(1 \pm \frac{T'}{\Pi}\right) - N_t(1 - e^{-z_t}),$$

$$N_{t+1} = N_t + \frac{\Delta N_t}{\Delta t} \cdot \Delta t,$$

where N_t is the numerical abundance of fish of a given species in year t; l is the time from hatching to about modal age in the fishery (taken as constant); α, β, and Π are constant coefficients. T' is perturbation sea temperature; Z_t is total instantaneous mortality, comprised of fishing, F_t, and natural mortality, M. (Perturbation sea temperature is just the difference, actual temperature for a given year minus the average temperature over several years.)

The model utilizes the Ricker (1954) stock–recruitment relationship and lumps individual year-classes. The input data are effort and sea temperature; the outputs are recruitment and abundance in numbers and catch in weight, e.g.,

$$(2)\quad \text{Catch}_t = \frac{F_t W}{Z_t} \cdot N_t(1 - e^{-z_t}),$$

where $F_t = qE_t$ = fishing pressure, the product of effort (E_t) and catchability (q), and W is the mean weight of individual fish caught for a fitted period. For purposes of interpretation, fishing effort is partitioned into "responsive" and "nonresponsive" components, i.e.,

$$(3)\quad E_{r,\,t+m} = kN_t,$$

where E_r is responsive effort, m is the lag required for fishermen to adjust to a perturbation in abundance, and k is a regression coefficient.

We propose to express environmental influence on recruitment with the factor, $1 \pm (T'/\Pi)$ (equation 1), and we are primarily concerned with the interactions of this structure in the model. This particular form is chosen for simplicity. It will be appropriate only for a narrow range of temperatures; however, we are using seasonal averages that exhibit a narrow range. Its biological origins are admittedly ambiguous. To what extent the environment acts directly on larvae physiologically as compared to its indirect influences on food supply through, for example, upwelling is uncertain. To introduce an actual, representative environmental index rather than a random noise simulator seems distinctly worthwhile. That this is indeed feasible is suggested by a growing body of work on the spatial coherence and temporal persistence of the ocean environment over the Scotian Shelf, e.g. Lauzier (1972), Sutcliffe et al. (1976, 1977).

Recruitment (R) with parameters α and β is affected by temperature with parameter Π (Fig. 1 and equation 1). Recruitment, natural mortality (M), and catch determine ΔN (which is used to update N). Abundance affects recruitment, catch, and a "responsive" portion, E_r, of the effort. The remainder of the effort signal, E_{nr}, is not "responsive" to abundance. Of course, we have only total fishing effort available as input data, but this will be discussed later.

In review, the model takes in ocean environment information which, together with stock abundance, is

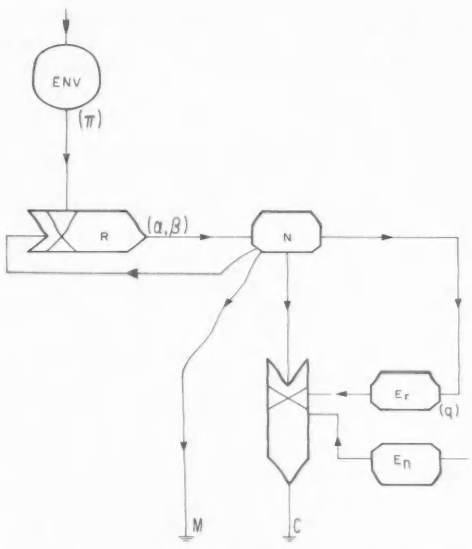

FIG. 1. Schematic diagram of fish population model (following the energy circuit language of Odum [1971]). The circle (environmental influence) indicates a source of energy. The large arrowheads denote multiplicative gates (abundance times environment, for recruitment, and abundance times effort, for catch). The hexagons (abundance and fishing effort) indicate self-maintaining populations (of fish and man). The sinks indicate natural mortality (M) and fishing mortality (catch). A point of interest is that the connection between abundance, N, and catch, C, may be either direct or indirect through responsive effort E_r.

transformed into numbers of recruits some years later. The recruits augment the stock abundance, while natural and fishing mortalities diminish stock abundance. Catch is computed on the basis of stock abundance and a given fishing effort. For purposes of comparison with available statistics, computed catch is converted from numbers to mass using the (constant) average weight of an individual.

If this model structure were found to provide useful insights, then we would be in position to examine the effects on fish stocks of persistent environmental perturbations.

Procedures

We compiled, where possible, information on recruitment, abundance, and catch. Recruitment information from virtual population analysis and from manipulation of current catch and effort data (i.e. Sissenwine 1974) was used for yellowtail flounder (*Limanda ferruginea*). Abundance information derived from surveys and from Baranov's equation (Ricker 1975, p. 13) was used. Catch statistics were available. In effect, our approach, rather than to produce an independent prediction of fish populations, has been to construct a synthesis of available information and to be guided by this overview in examining environmental influence on stock.

Using response-surface techniques (Davies 1956), we fitted values of α, β, and Π which, with temperature and effort as model inputs, produced abundances and catches to approximate those from the literature. Parameters yielding satisfactory correspondence between simulated and calculated abundances (judged graphically) were selected for further test runs. In the case of catch, the complete records of actual and simulated catches permitted comparison to be made by correlation and squared differences. Those parameter values were finally chosen that gave reasonable correspondence simultaneously in abundance and catch. Comparisons between simulated recruitment and values from the literature then were made where possible.

The provision of initial values for recruitment and abundance in the simulation model proved to be somewhat intricate. The recruits entering the fishery in year t at age l are simulated using their parent abundance for year, $t - l$ (e.g. equation 1). Consequently abundances for the previous l years had to be estimated before beginning the simulation. These were estimated from catch and effort data using equation (2) (the Baranov equation). After l years, simulated abundances become available for use in the calculation of recruitment. The lags (l) used were derived as in Sutcliffe et al. (1977) and amounted to 2 and 4 yr for yellowtail flounder and cod, respectively.

Results and Discussion

Data on fishing effort are often rather uncertain. Some reasons for this are that a fleet may catch two or more species and thus the fishing pressures on each are confounded (e.g. cod and haddock, Dickie 1965); also, the level of effort may be assessed after the fact based on catch (e.g. yellowtail flounder, Brown and Hennemuth 1971). Nevertheless we have partitioned the effort signal into "responsive" and "nonresponsive" components to facilitate interpretation; reasons for this will appear below.

"Responsive" effort is defined as

$$E_{r,l+m} = kN_l, \tag{3}$$

where m is the lag required for the fishing industry to adjust effort to a perturbation in fish abundance, and k is a regression coefficient, $k = r_{E,N}(\sigma_E/\sigma_N)$; $r_{E,N}$ is the correlation between E_{t+m} and N_t; σ_E and σ_N are standard devations of effort and abundance, respectively.

The responsive effort makes up a portion of the total determined by the correlation between total effort and abundance analogous to a feral predator–prey relationship. Nonresponsive effort is just the difference between the responsive component and the total.

YELLOWTAIL FLOUNDER

As a preliminary remark we find that Sissenwine (1974) has usefully modeled yellowtail empirically with temperature as the independent variable after rejecting stock–recruitment (biotic) processes as yielding poor fits.

Figure 2a shows plots of actual and simulated catch from our model for southern New England yellowtail

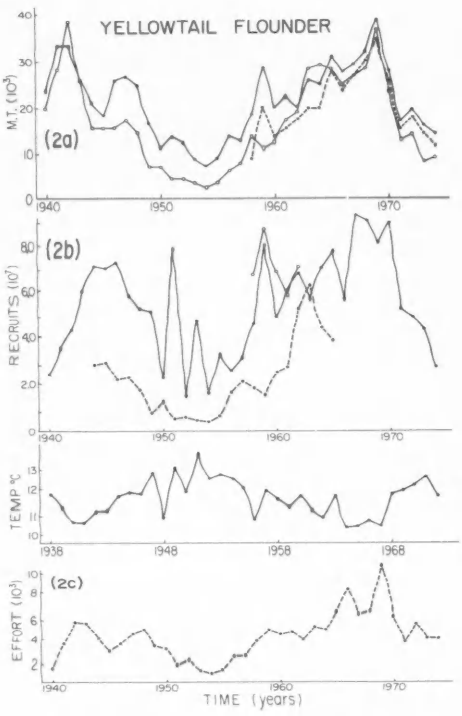

FIG. 2. Yellowtail flounder, southern New England. a, ○——○ Actual annual catch (Brown and Hennemuth [1971] and Edwards and Hennemuth [1975]), ●----● fitted, using $W = 0.4$ kg (Brown and Hennemuth 1971), $M = 0.1$, $q = 0.169$ (Sissenwine 1974), derived: $\alpha = 1.45$, $\beta = 9.15 \times 10^{-6}$, $\Pi = 2$; ●——● simulated (equation 1), b, Recruits, ●——● simulated, ●----● Sissenwine (1974), ○——○ Brown and Hennemuth (1971). c, Annual sea temperatures, ●——● St. Andrews, N.B. (June–October, Lauzier and Hull 1969 updated by Hull, personal communication); annual effort ●----● (Brown and Hennemuth 1971).

flounder. The parameters α, β, and Π derived from the fitted period 1956–74 were applied together with the time-series inputs, effort and sea temperature (see Fig. 2c), in the model (equation 1) to give the simulated catch of Fig. 2a.

Figure 2b shows our simulated recruitment plot with two comparisons. The general pattern is similar to that from Sissenwine's (1974) calculations and there is fair agreement to the 5 yr of data given by Brown and Hennemuth (1971) for virtual population analysis. The model operates near the peak of the Ricker stock–recruitment curve (Table 1).

The present model simulated annual catches over the entire period (1940–74) with $r = 0.907$ and over the fitted period (1958–74) with $r = 0.856$ with respect to actual catch. With the temperature input held constant (and parameter values unchanged), the latter drops to 0.385. With effort held constant (and the same parameter values), it drops to 0.237. Simple response analysis (Davies 1956) indicates that temperature is the main effect, effort is slightly less influential, and the effect of their interaction is minimal.

Temperature, representing the ocean environment as a whole, certainly plays an important role in yellowtail population dynamics. In this, our results confirm Sissenwine's (1974). However, we notice that the two signals driving the model, environment and effort, are themselves correlated (peak $r_{T,E} = -0.6$, span of 37 yr, E_{t+t+2} vs. T_t). This could occur by chance or because E_r is an important component; i.e. if catches per unit effort rise, then soon the fishery is more vigorously pursued. As previously noted, however, yellowtail effort statistics as presented in the literature are based in part on catch.

To compare the strengths of the two pathways (Fig. 1), abundance to catch directly and abundance through responsive effort (E_r) to catch, we apply the chain rule of partial differentiation and compare the magnitudes of the terms.

$$\frac{dC(N,E_r+E_{nr})}{dN} = \underbrace{\left.\frac{\partial C}{\partial N}\right|_{E=\text{constant}}}_{\text{direct path}} + \underbrace{\left.\frac{\partial C}{\partial E}\right|_{N=\text{constant}} \cdot \left\{\frac{\partial E_r}{\partial N} + \frac{\partial E_{nr}}{\partial N}\right\}}_{\text{indirect path}}$$

In words, catch is a function of abundance and effort. The total rate of change of catch with abundance is made up of the rate of change of catch with abundance alone plus the product, rate of change of catch with effort alone times the rate of change of (responsive) effort with abundance alone. (By definition nonresponsive effort does not change with abundance.) The first term measures the strength of the direct pathway. The second, product term measures the strength of the indirect pathway from abundance through responsive effort to catch.

The coefficient for the direct path (abundance to catch), evaluated at equilibrium, is

$$\left.\frac{\partial C}{\partial N}\right|_E = \frac{\bar{F}}{\bar{Z}}(1 - e^{-\bar{z}})$$

from equation (2). That over the indirect route is

$$\left.\frac{\partial C}{\partial E}\right|_N \cdot \frac{\partial E_r}{\partial N},$$

where

$$\left.\frac{\partial C}{\partial E}\right|_N = \frac{q\bar{N}}{\bar{Z}}(1 - e^{-\bar{z}}) \cdot \left[1 - \frac{\bar{F}}{\bar{Z}} + \frac{\bar{F}e^{-\bar{z}}}{1 - e^{-\bar{z}}}\right]$$

from equation (2), and

$$\frac{\partial E_r}{\partial N} = r_{E,N} \cdot \frac{\sigma_E}{\sigma_N}$$

from equation (3), where $r_{E,N}$ is the correlation between abundance and effort 2 yr subsequently.

The results using model-simulated abundance values (Table 1) are

$$\frac{\partial E_r}{\partial N} = 3.07 \times 10^{-8}$$

$$\left.\frac{\partial C}{\partial E}\right|_N = 8.41 \times 10^{+6}$$

$$\left.\frac{\partial C}{\partial N}\right|_E = 0.51$$

$$\left.\frac{\partial C}{\partial E}\right|_N \cdot \frac{\partial E_r}{\partial N} = 0.26$$

$$\frac{\left.\frac{\partial C}{\partial E}\right|_N \cdot \frac{\partial E_r}{\partial N}}{\left.\frac{\partial C}{\partial N}\right|_E} = 0.51$$

These indicate that the direct pathway is stronger in this case than the indirect pathway, but that both contribute constructively. The correlation between temperature and effort is suggested to result from the pathway (Fig. 1) temperature to abundance to responsive effort. In this pathway, too, the environmental factor plays a significant role.

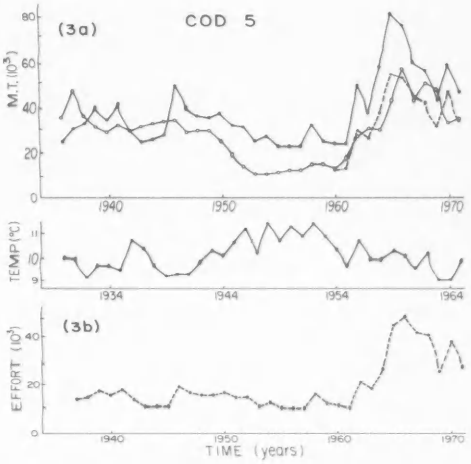

FIG. 3. Cod, ICNAF Subarea 5. a, ○——○ Actual annual catch (Brown and Heyerdahl 1972), ●----● fitted, using $W = 3.76$ kg, $M = 0.2$, $q = 0.0084$ (taken or calculated from Brown and Heyerdahl 1972), derived: $\alpha = 0.5$, $\beta = 7.15 \times 10^{-9}$, $\Pi = 6$; ●——● simulated (equation 1). b, Annual sea temperatures ●——● from St. Andrews, N.B. (July–December, Lauzier and Hull 1969 updated by Hull, personal communication); annual effort ●——● (Brown and Heyerdahl 1972).

COD

In Fig. 3a are seen comparisons of simulated and actual catch for ICNAF Subarea 5 cod. Treatment of data was as with yellowtail flounder except the fitted period is 1956–71. The model operates to the left of the peak of the Ricker stock–recruitment curve (Table 1).

TABLE 1. Model parameters and results.

	Yellowtail		Cod		
	1958–74 (fitted)	1940–74	1960–71 (fitted)	1936–71	1936–61
α	1.45	1.45 recruits/parent	0.5	0.5	0.5
β	9.15×10^{-9}	9.15×10^{-9} [parent]$^{-1}$	7.15×10^{-9}	7.15×10^{-9}	7.15×10^{-9}
Π	2	2°C	6	6	6
q	0.169	0.169 fraction stock caught / 1000 days fished	0.0084	0.0084	0.0084
M	0.1	0.1 fraction dying/yr	0.2	0.2	0.2
r_{TC}	0.856	0.907	0.804	0.67	0.45
$\bar{N}$	8.4×10^7	11×10^7 fish	4.65×10^7	8×10^7	8.7×10^7
σ_N		2.4×10^7 fish			0.50×10^7
$\bar{E}$		4490 days fished			13.2
σ_E		2000 days fished			2.8
r_{EN}		0.372			0.64

The model simulates catches over the entire record (1936–71), $r = 0.670$, and the fitted period, $r = 0.804$, with actual catch. With temperature input held constant, $r = 0.807$; with effort held constant, $r = 0.31$. In these tests, parameter values are unchanged from those given in Fig. 3a. Simple response analysis indicates that effort is the main driver and that the smaller effects of temperature and temperature–effort interaction counteract.

The peak correlation between temperature and cod effort ($r_{T,E} = -0.7$) is delayed 2 yr behind that between temperature and catch for a total of 6 yr lag over 1931–61.

Calculations of the strengths of pathways for 1936–59 yield

$$\frac{\partial E_r}{\partial N} = 3.6 \times 10^{-7}$$

$$\left.\frac{\partial C}{\partial E}\right|_N = 6.0 \times 10^{5}$$

$$\left.\frac{\partial C}{\partial N}\right|_E = 9.5 \times 10^{-2}$$

$$\left.\frac{\partial C}{\partial E}\right|_N \cdot \frac{\partial E_r}{\partial N} = 0.22$$

$$\frac{\left.\frac{\partial C}{\partial E}\right|_N \cdot \frac{\partial E_r}{\partial N}}{\left.\frac{\partial C}{\partial N}\right|_E} = 2.2$$

These results show that the indirect pathway via responsive effort is more important than the direct pathway. The indirect pathway involves E_r responding to abundance which responds to temperature. Since a considerable fraction, 38%, of the total effort variance is provided by E_r and since the environmental effect is reflected in E_r, this model temperature structure is deemed to be significant. The period 1960–71 was excluded from this latter analysis because of a greatly increased effort from large foreign fleets quite unlike the previous pattern.

To confirm the above interpretation, the effort signal was actually partitioned into responsive and nonresponsive components (equation 3). Using the latter component only, the model was run over 1931–61; the simulated catches did not correspond to actuality ($r = 0.15$). Responsive effort is implied to be important. In effect, environmental variability, mediated by abundance, is sensed and amplified by responsive effort with the result that catch shows strong relationship to environment (sea temperature).

Conclusions

The role of the environmental modification in the simulation model presented turns out to be significant, sometimes subtly so. In yellowtail flounder where reliance upon recruits is heavy the effect of environment upon catch is direct. In cod where the effects of recruitment variability are buffered by the presence of more year-classes but where the fishery may be prosecuted by a perceptive fishing industry akin to a natural predator–prey system, the effect of environment upon catch is amplified, and that upon abundance is stabilized, through responsive effort. Where nonresponsive effort is dominant, environmental influence may be overshadowed (e.g. cod, 1962–71).

On balance, some environmental and responsive effort modifications such as presented seem worth preserving in models of these fish stocks. Opportunities are thereby opened for examination of stock abundance relative to various effort strategies (e.g. more or less responsive) amidst environmental perturbations.

Acknowledgments

Our special thanks to A. Orr and R. Smith for assistance and helpful discussions; to W. Silvert for financial support and helpful discussions; to P. Lett for comments; to S. Kerr for patient advice; and to L. Dickie for his cheerful encouragement.

BROWN, B. E., AND R. C. HENNEMUTH. 1971. Assessment of the yellowtail flounder fishery. Int. Comm. Northwest Atl. Fish. Res. Doc. 71/14: 57 p.

BROWN, B. E., AND E. G. HEYERDAHL. 1972. An assessment of the Georges Bank cod stock (Div. 5Z). Int. Comm. Northwest Atl. Fish. Res. Doc. 72/117: 24 p.

DAVIES, O. L. 1956. Design and analysis of industrial experiments. Oliver and Boyd, Edinburgh. 636 p.

DICKIE, L. M. 1965. Difficulties in interpreting trends in cod and haddock landings from the eastern Scotian Shelf. Int. Comm. Northwest Atl. Fish. Res. Bull. 2: 80–82.

EDWARDS, R., AND R. C. HENNEMUTH. 1975. Maximum yield: Assessment and attainment. Oceanus 18(2): 3–9.

LAUZIER, L. M. 1972. Climatic change in the marine subarctic. Trans. R. Soc. Can. 10 (Ser. 4): 297–307.

LAUZIER, L. M., AND J. H. HULL. 1969. Coastal station data temperatures along the Canadian Atlantic coast, 1921–1969. Fish. Res. Board Can. Tech. Rep. 150: 25 p.

ODUM, H. T. 1971. Environment, power and society. Wiley-Interscience, Inc., New York, N.Y. 331 p.

RICKER, W. E. 1954. Stock and recruitment. J. Fish. Res. Board Can. 11: 559–623.

1975. Computation and interpretation of biological statistics of fish populations. Bull. Fish. Res. Board Can. 191: 382 p.

SCHAEFER, M. B. 1954. Some aspects of the dynamics of populations important to the management of the commercial marine fisheries. Inter-Am. Trop. Tuna Comm. Bull. 1(2): 27–56.

SISSENWINE, M. P. 1974. Variability in recruitment and equilibrium catch of the Southern New England yellowtail flounder fishery. J. Cons. Int. Explor. Mer. 36: 15–26.

SUTCLIFFE, W. H. JR. 1972. Some relations of land drainage, nutrients, particulate material and fish catch in two eastern Canadian bays. J. Fish. Res. Board Can. 29: 357–362.

1973. Correlations between seasonal river discharge and local landings of American lobster (*Homarus americanus*) and Atlantic halibut (*Hippoglossus hippoglossus*) in the Gulf of St. Lawrence. J. Fish. Res. Board Can. 30: 856–859.

SUTCLIFFE, W. H. JR., K. DRINKWATER, AND B. S. MUIR. 1977. Correlations of fish catch and environmental factors in the Gulf of Maine. J. Fish. Res. Board Can. 34: 19–30.

SUTCLIFFE, W. H. JR., R. H. LOUCKS, AND K. F. DRINKWATER. 1976. Coastal circulation and physical oceanography of the Scotian Shelf and the Gulf of Maine. J. Fish. Res. Board Can. 33: 98–115.

Sorption of Arsenic and Cadmium and Their Effects on Growth, Micronutrient Utilization, and Photosynthetic Pigment Composition of *Asterionella formosa*

H. L. CONWAY

Ecological Sciences Section, Radiological and Environmental Research Division, Argonne National Laboratory, Argonne, Ill. 60439, USA

CONWAY, H. L. 1978. Sorption of arsenic and cadmium and their effects on growth, micronutrient utilization, and photosynthetic pigment composition of *Asterionella formosa*. J. Fish. Res. Board Can. 35: 286–294.

By use of continuous-culture techniques, populations of the freshwater diatom *Asterionella formosa* were exposed to various concentrations of arsenic or cadmium for periods of 6–23 days. Sorption of arsenic (as arsenate) was a linear function of ambient concentrations $<130\ \mu g\ As \cdot L^{-1}$ but reached an apparent plateau at ambient values $>130\ \mu g\ As \cdot L^{-1}$. In contrast, cadmium sorption was a complex function of ambient concentration and time. Cellular arsenic and cadmium was desorbed in some of the experiments, and there appeared to be an active regulatory mechanism that kept the cellular arsenic content at a nontoxic level. For arsenic, no detrimental effects on growth or on micronutrient utilization were observed over the range of ambient concentrations used ($<160\ \mu g\ As \cdot L^{-1}$). For cadmium, however, an ambient concentration of $\sim 2\ \mu g\ Cd \cdot L^{-1}$ reduced the population growth rate by an order of magnitude, while populations exposed to $>10\ \mu g\ Cd \cdot L^{-1}$ ceased growth and micronutrient utilization in 20–30 h. Fractionation experiments suggest that a large proportion of the cellular arsenic was associated with the organic layer surrounding the frustule, while most of the cellular cadmium was associated with the cell contents.

Key words: arsenic, cadmium, toxicity, sorption, diatom, *Asterionella formosa*

CONWAY, H. L. 1978. Sorption of arsenic and cadmium and their effects on growth, micronutrient utilization, and photosynthetic pigment composition of *Asterionella formosa*. J. Fish. Res. Board Can. 35: 286–294.

Nous servant de techniques de culture continue, nous avons exposé des populations de la diatomée d'eau douce *Asterionella formosa* à diverses concentrations d'arsenic et de cadmium pendant des périodes de 6 à 23 jours. La sorption de l'arsenic (comme arséniate) est fonction linéaire de concentrations ambiantes de $<130\ \mu g\ As \cdot L^{-1}$ mais atteint un plateau apparent à des valeurs de $>130\ \mu g\ As \cdot L^{-1}$. Par contraste, la sorption du cadmium est fonction complexe de la concentration ambiante et du temps. L'arsenic et le cadmium cellulaires sont désorbés dans quelques-unes des expériences, et il semble y avoir un mécanisme régulateur actif qui maintient la concentration d'arsenic cellulaire à un niveau non toxique. Pour ce qui est de l'arsenic, nous n'avons observé aucun effet nuisible ni sur la croissance ni sur l'utilisation des oligo-éléments dans la gamme des concentrations ambiantes utilisées ($<160\ \mu g\ As \cdot L^{-1}$). Pour ce qui est du cadmium, cependant, une concentration ambiante de $\sim 2\ \mu g\ Cd \cdot L^{-1}$ abaisse le taux de croissance de la population d'un ordre de grandeur, alors que chez les populations exposées à $>10\ \mu g\ Cd \cdot L^{-1}$ la croissance et l'utilisation des oligo-éléments cessent en 20 à 30 h. Des expériences de fractionnement suggèrent qu'une forte proportion de l'arsenic cellulaire est associé à la couche organique qui entoure la frustule, alors que la plus grande partie du cadmium cellulaire est associé aux contenus cellulaires.

Received July 13, 1977
Accepted December 5, 1977

Reçu le 13 juillet 1977
Accepté le 5 décembre 1977

MANY trace elements are released to the environment from fossil fuels, pesticides, and certain industrial processes such as electroplating or the manufacture of paints and plastics. These materials are introduced into the Great Lakes by wet and dry deposition from the atmosphere and by surface runoff from surrounding watersheds (e.g. Shiami and Kuntz 1973; Winchester and Nifong 1971). Although some of these trace ele-

Printed in Canada (J4921)
Imprimé au Canada (J4921)

TABLE 1. Comparison of the major ions and micronutrients in synthetic Lake Michigan water (SLMW) and natural Lake Michigan water (LMW).

	SLMW	LMW	Source
Ca	32 mg·L^{-1}	32 mg·L^{-1}	Weiler and Chawla (1969)
Mg	10 mg·L^{-1}	10 mg·L^{-1}	Weiler and Chawla (1969)
Cl	72 mg·L^{-1}	6.2 mg·L^{-1}	Weiler and Chawla (1969)
SO_4	20 mg·L^{-1}	16 mg·L^{-1}	Weiler and Chawla (1969)
Na	50 mg·L^{-1}	3.4 mg·L^{-1}	Weiler and Chawla (1969)
K	1 mg·L^{-1}	0.9 mg·L^{-1}	Weiler and Chawla (1969)
HCO_3	130 mg·L^{-1}	130 mg·L^{-1}	Weiler and Chawla (1969)
Si as SiO_4	280 μg·L^{-1} (10 μmol·L^{-1})	480 μg·L^{-1} (17 μmol·L^{-1})	Conway et al. (1977)
N as NO_3	265 μg·L^{-1} (19 μmol·L^{-1})	280 μg·L^{-1} (20 μmol·L^{-1})	Unpublished data
N as NH_4	7 μg·L^{-1} (0.5 μmol·L^{-1})	3 μg·L^{-1} (0.2 μmol·L^{-1})	Unpublished data
P as PO_4	10 μg·L^{-1} (0.3 μmol·L^{-1})	<3 μg·L^{-1} (<0.1 μmol·L^{-1})	Unpublished data
B as BO_3	90μg·L^{-1}	not available	

ments are required for normal growth and reproduction of aquatic organisms, others are toxic (Leland et al. 1974; O'Kelley 1974).

The chemical behavior of nonessential trace elements is often similar to that of essential ones. Cadmium, for example, often replaces zinc in metalloenzymes, much to the detriment of the cell (Applebury et al. 1970). Cadmium not only inhibits a large number of metabolic enzyme systems but also complexes with amino acids, peptides, and proteins (Vallee and Ulmer 1972), and it markedly affects the conformation of polyriboadenylic acid (Eickhorn et al. 1971) and the physical properties of DNA (Miller 1970). Thus, many sites exist at which cadmium may be detrimental to the metabolic processes of organisms.

Arsenic (as arsenate) is chemically similar to phosphate and the two ions can compete for phosphate permease sites during entry into the cell (Jung and Rothstein 1965; Button et al. 1973). Arsenate is known to act as an "uncoupler" by competing with phosphorus in the formation of organic esters in the main metabolic pathways and it is found in algae as lipid and water-soluble arseno-organic compounds (Lunde 1973).

Little is known about the chronic effects of arsenic and cadmium on phytoplankton. The objective of this study was (1) to assess the effects of arsenic and cadmium on the growth, micronutrient utilization, and photosynthetic pigment composition of *Asterionella formosa*, (2) to determine the sorption characteristics of arsenic and cadmium, and (3) to document the sites of cellular accumulation of these potentially toxic trace elements.

Materials and Methods

Culture Medium

An automated method for the synthesis of continuous-culture medium was developed for use in these experiments. A synthetic medium similar to natural Lake Michigan water was used (Table 1). The pH of the synthetic Lake Michigan water (SLMW) was ~8.2 with a buffering capacity similar to natural Lake Michigan water (LMW).

The three 4-L bottles contain the concentrated ionic solutions: (I) trace metal and micronutrient stock; (II) $MgSO_4$, $MgCl_2$, $NaHCO_3$, KCl, and H_3BO_3; and (III) $CaCl_2$ (*Fig. 1*). *The three ionic solutions, deionized water* (D.I. water), and air are mixed together and transferred to a *20-L storage carboy by a peristaltic proportioning pump.* The pump and the solenoid valve are activated when the medium in the 20-L reservoir drops below a given level. Trace metals and vitamins in the SLMW were maintained at the $f/50$ concentration of Guillard and Ryther (1962). *Sodium ferric diethylenetriamine pentaacetate (~0.2*

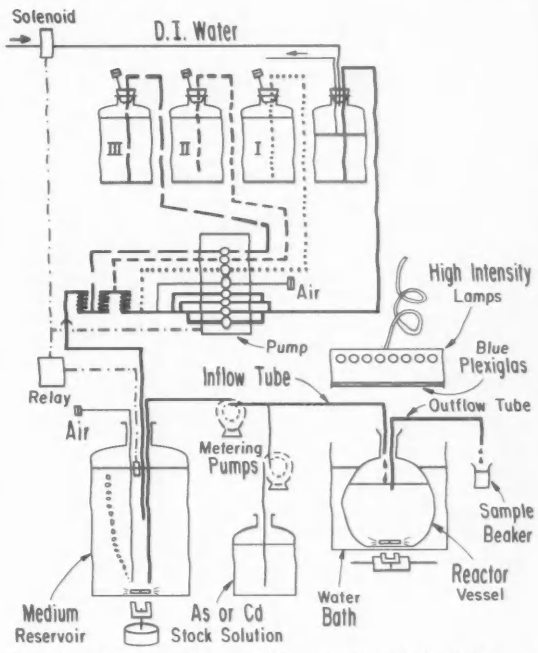

FIG. 1. Apparatus for supplying synthetic Lake Michigan water and the arsenic or cadmium stock solution to the reactor vessel in which the *Asterionella formosa* population is grown.

TABLE 2. Coefficients of variation for analyses used in this study; n represents the number of replicates.

Analysis		Units	Coefficient of variation ($\sigma/\bar{x}$)	n
Cellular photosynthetic pigment content	Chlorophyll *a* (total)	$\mu g \cdot (10^9\ \mu m^3)^{-1}$	8%	7
	Carotene	$\mu g \cdot (10^9\ \mu m^3)^{-1}$	20%	7
Micronutrient utilization	Nitrogen	$\mu mol\ N \cdot (10^9\ \mu m^3)^{-1}$	2%	10
	Silicon	$\mu mol\ Si \cdot (10^9\ \mu m^3)^{-1}$	2%	10
	Phosphorus	$\mu mol\ P \cdot (10^9\ \mu m^3)^{-1}$	5%	10
Cellular arsenic content		$\mu g\ As \cdot (10^9\ \mu m^3)^{-1}$	12%	7
Cellular cadmium content		$\mu g\ Cd \cdot (10^9\ \mu m^3)^{-1}$	5%	10
Ambient arsenic concn		$\mu g \cdot L^{-1}$	1%	10
Ambient cadmium concn		$\mu g \cdot L^{-1}$	1%	10
Population biovolume		$10^9\ \mu m^3 \cdot L^{-1}$	2%	10

$mg \cdot L^{-1}$) was present in the SLMW; however, the stability constant of this organic ligand would make it highly unlikely that iron would be replaced by cadmium (Sillen and Martell 1964).

Synthetic Lake Michigan water was pumped into each reactor vessel at a dilution rate of $0.02 \cdot h^{-1}$ by a positive displacement metering pump (Fig. 1). The reactor vessels were 6-L boiling flasks sealed with neoprene rubber stoppers so that a constant volume could be maintained inside the flasks. Switching valves in the influent and effluent lines allowed the flow to be diverted for sampling. The cultures were stirred with Teflon®-coated magnetic stirring bars with polyethylene Quick Disconnects® on the ends to increase stirring efficiency. The reactor vessels were placed in a water bath regulated to 15.0 ± 0.1°C. The lighting system consisted of high-intensity fluorescent lights approximately 15 cm above the reactor vessel. A sheet of blue Plexiglass®, 0.4 cm thick, was placed directly below the lights to modify the spectrum and make it comparable to 5-m underwater light (Holmes 1957). The resulting light intensity at the culture vessel was ~ 0.08 g-cal $\cdot cm^{-2} \cdot min^{-1}$ ($\sim$14,000 lx); continuous light was used in all experiments.

Experimental Procedure and Analyses

Populations of *Asterionella formosa* were grown in three chemostats under silicate limitation until a steady state was reached (i.e. $dx/dt = 0$ in equation 1). A solution of radioactive plus stable arsenic (as arsenate) was then continuously added (via a metering pump) to the influent of one chemostat (see Fig. 1), while a second chemostat population was similarly treated with a cadmium (Cd^{+2}) solution (radioactive plus stable); the population of the third chemostat was used as a control. The three reactors were sampled 2 or 3 times a day for total population biovolume (using a Coulter counter, TA-II®), micronutrient concentrations, sorption of arsenic or cadmium by *A. formosa*, and ambient concentrations of arsenic or cadmium in the reactors. The influent was analyzed daily for concentrations of micronutrients and arsenic or cadmium. Duplicate samples were taken for all analyses. Radioactive arsenic (^{74}As) and cadmium (^{115m}Cd) were counted on a Packard® liquid-scintillation spectrometer. Particulate samples (*A. formosa* cells) were collected on 0.45-μm Millipore® filters which were then placed in a scintillator containing 4 g PPO(2,5-diphenyloxazole), 0.05 g POPOP (1,4-bis-[2-(5-phenyloxazolyl)]-benzene), 120 g naphthalene, and sufficient 1,4-dioxane to make 1 L of solution. Influent samples and the filtrate from the particulate samples were prepared by adding 1 mL of liquid to the scintillator. Specific activities in the three experiments ranged from 2.1×10^{-2} to 5.0×10^{-2} $\mu Ci \cdot \mu g^{-1}$ for ^{74}As, and 2.0×10^{-3} to $3.3\ \mu Ci \cdot \mu g^{-1}$ for ^{115m}Cd. (The specific activity was determined by dividing the total activity of ^{74}As or ^{115m}Cd (μCi) by the total weight of stable arsenic or cadmium (μg) in the stock solution.) Micronutrient utilization was defined as influent concentration minus effluent concentration. Cellular arsenic and cadmium concentrations as well as micronutrient utilization and photosynthetic pigments were normalized to population cell volume (the average biovolume per cell was $\sim 360\ \mu m^3$).

Micronutrient analyses were made using an autoanalyzer system. Nitrate and silicate analysis methods were those given by Armstrong et al. (1967); the phosphate method was that of Murphy and Riley (1962) as automated by Hager et al. (1968). Photosynthetic pigments were determined by the methods described in Strickland and Parsons (1972). Sampling procedure and resulting analyses were repeated 7 or 10 times to determine variability (Table 2).

The pH of the effluent was measured 2–3 times during the course of an experiment; values ranged from $\sim$8.0 to $\sim$8.5. The effect of a changing pH (pH 6 to pH 9) had a minimal effect on the percent of the free cadmium ion (Cd^{+2}) (89 to 94%, respectively) in a chemical equilibrium model of "normal" Great Lake water (Childs 1971).

The growth rate in the reactor vessel was determined from changes in population biovolume by use of an integrated form of the equation

$$dx/dt = (\mu - D)x, \tag{1}$$

where x is the population biovolume ($\mu m^3 \cdot L^{-1}$) at time t, $D = f/v$ is the dilution rate, f being the rate ($mL \cdot h^{-1}$) at which the medium flows into the reactor and v is the volume (mL) in the reactor, and μ is the specific growth rate (h^{-1}). When $\mu = D$, it follows that $dx/dt = 0$; i.e. a steady state condition has been attained. Integrating equation (1) and solving for μ yields

$$\mu = D + (1/t) \ln (x/x_0). \tag{2}$$

A complete discussion of chemostat theory can be found in Kubitschek (1970).

Three experiments were conducted with three different influent concentrations of arsenic or cadmium and are designated I ($\sim 8\ \mu g\ As \cdot L^{-1}$; $\sim 2\ \mu g\ Cd \cdot L^{-1}$), II ($\sim 60\ \mu g\ As \cdot L^{-1}$; $\sim 10\ \mu g\ Cd \cdot L^{-1}$), and III ($\sim 160\ \mu g\ As \cdot L^{-1}$; $\sim 20\ \mu g\ Cd \cdot L^{-1}$).

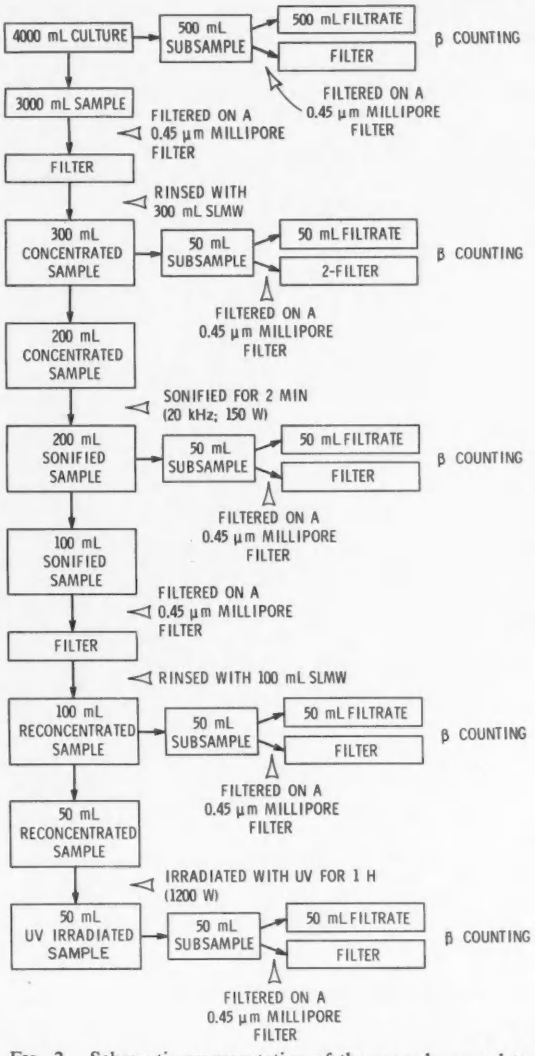

FIG. 2. Schematic representation of the procedure used to determine the site of arsenic or cadmium in/on *Asterionella formosa* cells.

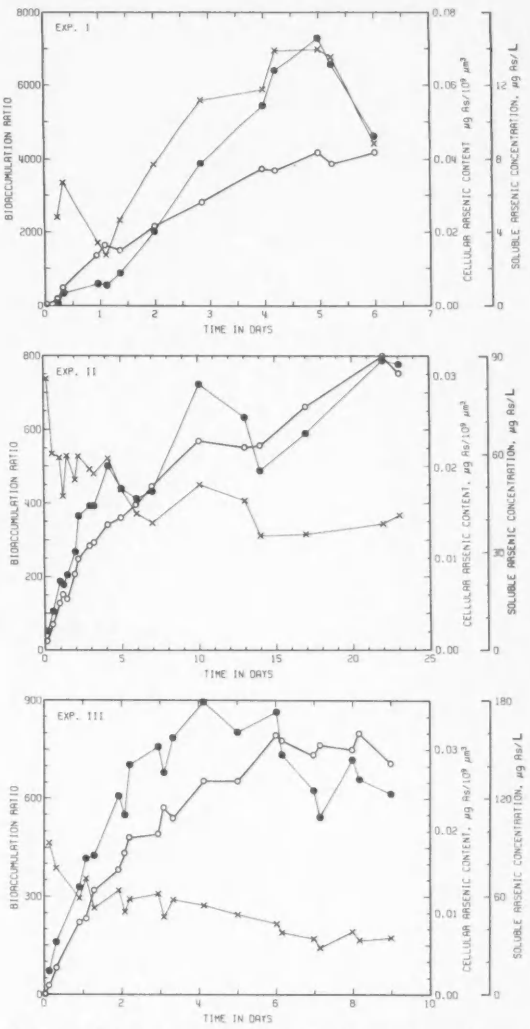

FIG. 3. Cellular arsenic content (●), ambient arsenic concentration (○), and bioaccumulation ratio (×) vs. time for Experiments I, II, and III. Influent arsenic concentrations were ~8 μg As·L^{-1} in I, ~60 μg As·L^{-1} in II, and ~160 μg As·L^{-1} in III. BR = (concentration in or on organism) · (concentration in medium)$^{-1}$.

A procedure was developed to determine the location of arsenic or cadmium in or on the diatom cells (Fig. 2). Sonification (~150 W, 20 kHz) separated the cell contents from the frustule and its organic coating; the separation was checked by microscopic examination. Subsequent irradiation of the frustules with high-intensity ultraviolet light (1200 W) oxidized the organic coating, leaving the cleaned frustule. Measurements of the activity of ^{74}As or ^{115m}Cd, made at various stages during this fractionating process, made it possible to estimate the proportion of arsenic or cadmium associated with the cell contents, the organic coating of the frustule, and the cleaned frustule. The samples were processed as rapidly as possible to reduce the possibility of redistribution of arsenic or cadmium during the fractionation procedure.

Results and Discussion

ARSENIC

The cellular arsenic content appeared to reach a quasi-equilibrium value of ~0.03 μg As·(10^9 μm^3)$^{-1}$

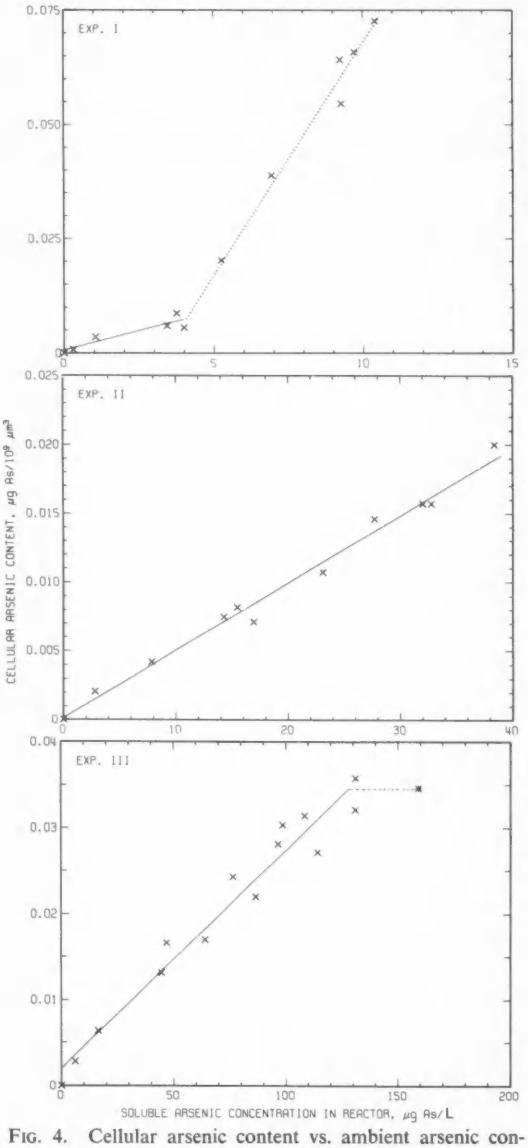

FIG. 4. Cellular arsenic content vs. ambient arsenic concentration for Experiments I, II, and III. Data point designated (*) in III was not used in fitting the straight line to the data.

after day 22 in Experiment II and from day 4 to 6 in Experiment III (Fig. 3). The cellular cadmium content in Experiment I was higher than in the other two experiments and a quasi-equilibrium was not reached; however, the population was rapidly releasing arsenic at the end of the experiment and may have attained the quasi-equilibrium value of $\sim 0.03\ \mu g\ As \cdot (10^9\ \mu m^3)^{-1}$ if the test had been extended. An apparent release of cellular arsenic was observed after day 5 in Experiment I and after day 6 in Experiment III, corresponding to a "plateau" in the ambient arsenic concentration. Except for Experiment I, the BR decreased from an initial peak value to a quasi-equilibrium value towards the end of the experiment. In Experiment I the BR exhibited an initial peak value, declined briefly, and then seemed to follow the cellular arsenic content.

The sorption of arsenic for each experiment appeared to be a linear function of ambient arsenic concentrations at levels $<130\ \mu g \cdot L^{-1}$ (Fig. 4). In Experiment II, the values $>40\ \mu g\ As \cdot L^{-1}$ were not plotted because of a large increase in the influent arsenic concentration that affected the quasi-equilibrium of the system. The line had a different slope for each experiment: $b = 0.00025$ in Experiment III and $b = 0.00049$ in Experiment II, while in Experiment I it shifted from $b = 0.0017$ ($<4\ \mu g\ As \cdot L^{-1}$) to $b = 0.0102$ ($>4\ \mu g\ As \cdot L^{-1}$). For ambient arsenic concentrations >4 and $<130\ \mu g \cdot L^{-1}$, the lowest slope value (Experiment III) corresponded to the highest influx of arsenic into the reactor ($\sim 19\ \mu g\ As \cdot h^{-1}$), while the highest slope value (Experiment I) corresponded to the lowest influx ($\sim 1\ \mu g\ As \cdot h^{-1}$). This relationship supports the idea that the cells were able to utilize the ambient arsenic more effectively at the lowest flux rate. The change in the slope of the line during Experiment I, however, may have been the result of competition with phosphorus for entry into the cell. Arsenate is known to enter yeast cells via the transport system that is normally responsible for phosphate uptake, so the two chemically similar ions compete for entry (see Jung and Rothstein 1965; Button et al. 1973). Thus, since phosphate at a concentration $<0.1\ \mu mol \cdot L^{-1}$ was present in the medium, the change of slope at $\sim 4\ \mu g \cdot L^{-1}$ ($\sim 0.05\ \mu mol \cdot L^{-1}$ arsenic as arsenate) may indicate that above this concentration the uptake of arsenic is inhibited to a lesser degree by the phosphate level in the medium.

The leveling off in the cellular arsenic content at ambient arsenic levels above $130\ \mu g \cdot L^{-1}$ (Fig. 4, Experiment III) may be due to saturation of arsenic sorption sites, though the evidence is only a single "saturation" data point. *Asterionella formosa* appears to have a mechanism to maintain the cellular arsenic content at a nontoxic level of $\sim 0.03\ \mu g\ As \cdot (10^9\ \mu m^3)^{-1}$ (Experiments II and III).

One possible explanation for the decrease in BR values, following the high initial value observed in Experiments II and III, is activation of an enzymatic transport system that excretes a portion of the arsenate ions back into the medium. Similarly, the relatively low percentage of arsenic found in the cell contents (see below) indicates the presence of an arsenate excretory system. However, desorption of arsenic has been observed for yeast cells (Jung and Rothstein 1965) and this may have been the mechanism that resulted in the loss of cellular arsenic and the low percentage of arsenic in the cell contents. The cellular arsenic content

TABLE 3. Photosynthetic pigments, cellular content (As and Cd), and ambient concentration (As and Cd), at the end of Experiments II and III. NA = not applicable.

	Photosynthetic pigments $\mu g \cdot (10^9\ \mu m^3)^{-1}$		Cellular content $\mu g \cdot (10^9\ \mu m^3)^{-1}$	Ambient concn $\mu g \cdot L^{-1}$	Duration of expt (days)
	Chl *a* (total)	Carotene			
			Experiment II		
As	0.76	2.28	0.03	60	24
Cd	0.08	0.15	0.39	10	24
Control	1.58	3.02	NA	NA	24
			Experiment III		
As	2.40	2.70	0.03	150	10
Cd	0.64	1.46	0.89	20	10
Control	2.19	2.70	NA	NA	10

of $\sim 0.03\ \mu g\ As \cdot (10^9\ \mu m^3)^{-1}$ corresponds to a bioaccumulation ratio of ~250. Bioaccumulation ratios of ~1500 (Copeland and Ayres 1972) and ~3500 (Seydel 1972) have been observed for natural phytoplankton samples from Lake Michigan; however, what fraction of the total phytoplankton biomass was *A. formosa* is not known.

Ambient arsenic concentrations below $160\ \mu g \cdot L^{-1}$ did not affect the rates of growth or micronutrient utilization of *A. formosa*; i.e. growth and micronutrient utilization were not significantly different from those observed for the control population. The cellular content of photosynthetic pigments decreased by more than 1 SD after a 24-day exposure to arsenic (Table 3).

CADMIUM

The cellular cadmium content did not attain an equilibrium value in Experiments I and II even though a "plateau" in the ambient cadmium concentration had been reached by day 5 (Fig. 5). In Experiment III the cellular cadmium content did appear to reach a quasi-equilibrium value after the influent was shut off on day 5. The influent was shut off on day 5 in Experiments II and III because the growth rate of the population was less than the dilution rate and the population biomass was decreasing ($\mu < D$). A subsequent release of a portion of the cell-bound cadmium was observed after day 7 in Experiment III. The temporal change of BR was similar to that observed for the cellular cadmium content in each experiment.

The sorption of cadmium appeared to be a complex function of time and ambient cadmium concentration and continued even after the ambient concentration was constant (Fig. 6 and 7) and the cells had ceased growing (e.g. $\mu \Rightarrow 0$; see below). Desorption observed during the latter portion of Experiment III suggests that a saturation value may have been attained, though it may have been the result of chelation by extracellular metabolites as observed by Cossa (1976), using *Phaeodactylum tricornutum*. The cadmium sorption data were submitted to a Freundlich isotherm analysis but they failed to conform to this empirical description of a pure adsorption process. Detailed analysis of cadmium sorption kinetics as a function of time and ambient concentration, which will be treated in a later paper (Conway and Williams unpublished data), implies that it is a combination of active and passive processes and this may in turn account for the failure to conform to the Freundlich isotherm formulation.

Cossa (1976) found BR ≈ 10,000 for *P. tricornutum* at an ambient concentration of $10\ \mu g\ Cd \cdot L^{-1}$. The cellular cadmium content at the end of Experiment II ($\sim 0.8\ \mu g\ Cd \cdot (10^9\ \mu m^3)^{-1}$ at $\sim 10\ \mu g\ Cd \cdot L^{-1}$) corresponded to a BR of ≈40,000. Although Cossa observed a significantly lower BR in his study, he worked with a marine diatom that was grown in batch culture. Recent studies at this laboratory have shown that the BR of cadmium for *A. formosa* is ~3 times greater than that observed for *Fragilaria crotonensis*, another freshwater diatom (Conway and Williams unpublished data).

In Experiment I an order of magnitude reduction in the growth rate was observed at an ambient concentration of $\sim 2\ \mu g\ Cd \cdot L^{-1}$ (Fig. 6), while in Experiment II and III the growth rate became too small to measure (e.g. $\mu \Rightarrow 0$) after day 6 which corresponded to ambient cadmium concentrations $> 10\ \mu g \cdot L^{-1}$. Growth rates began decreasing before day 2 in Experiment II and III, and after day 2 in Experiment I. The data in Table 4 indicate that neither ambient cadmium concentration nor cellular cadmium content is the single factor controlling the growth rate. The growth rate of this organism was apparently affected by a combination of these two factors as well as the duration of the exposure.

The utilization of phosphate (and silicate in Experiment III) was greater than that for the control during the time before the drastic reduction (cessation) of the growth rate (Fig. 8 and Table 5). The disruption and eventual inactivation of the micronutrient transport and/or assimilatory enzyme systems were apparent in the populations exposed to cadmium. The enhanced

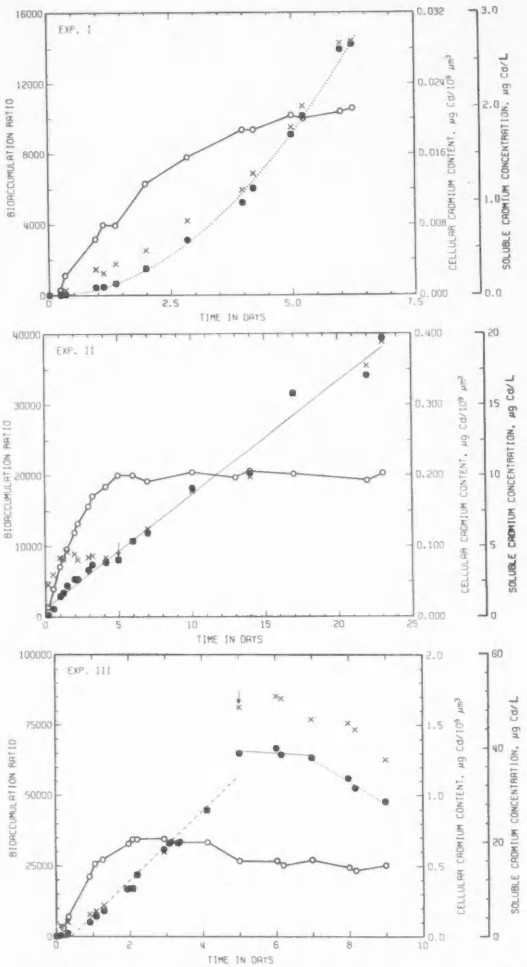

FIG. 5. Cellular cadmium content (●), ambient cadmium concentration (○), and bioaccumulation ratio (×) vs. time for Experiments I, II, and III. Influent cadmium concentrations were ~2 μg Cd·L⁻¹ in I, ~10 μg Cd·L⁻¹ in II, and ~20 μg Cd·L⁻¹ in III. Arrow (↓) indicates the point at which the influent was shut off. The line was fitted to data points for cellular cadmium content.

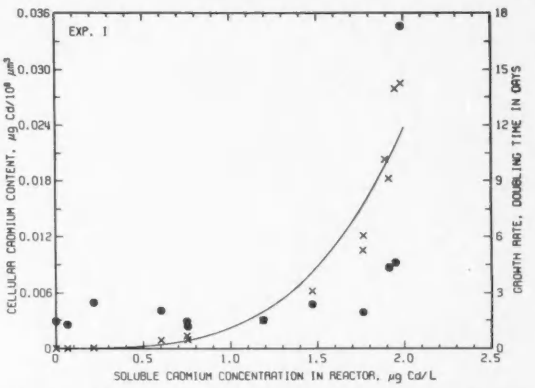
EXP. I
CELLULAR CADMIUM CONTENT, μg Cd/10⁹ μm³
GROWTH RATE, DOUBLING TIME IN DAYS
SOLUBLE CADMIUM CONCENTRATION IN REACTOR, μg Cd/L

FIG. 6. Cellular cadmium content (×) and growth rate (●) expressed as doubling time in days, vs. ambient cadmium concentration for Experiment I. The line was fitted to data points for cellular cadmium content.

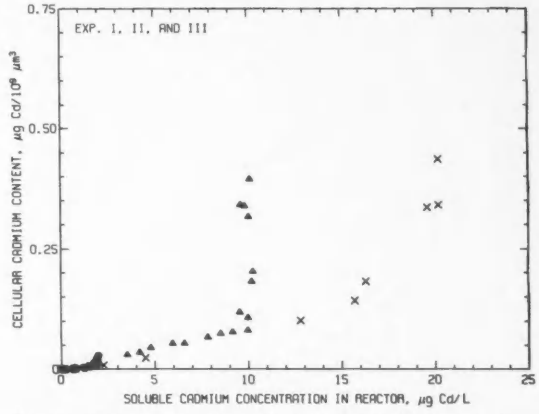

FIG. 7. Cellular cadmium content vs. ambient cadmium concentration for the three experiments: ● for Experiment I, ▲ for Experiment II, and × for Experiment III.

uptake of phosphate (and in Experiment III, silicate) prior to the eventual cessation may indicate a breakdown in the feedback control of the permease system that transports phosphate (or silicate) into the cell. This is similar to a mechanism postulated for ammonium inhibition of nitrate uptake (Conway 1977) and for the initial surge in micronutrient utilization by nutrient-limited populations (Conway et al. 1976; Conway and Harrison 1977).

The photosynthetic pigments in the populations exposed to cadmium were significantly lower than that in the control population (Table 3). Although the cellular and ambient cadmium levels were higher in Experiment III, the most pronounced effect on the photosynthetic pigments occurred in Experiment II, evidently because the time of exposure to cadmium was 2.4 times as long in Experiment II. The photosynthetic pigment content of the population exposed to cadmium was reduced by more than an order of magnitude compared with the control population; as with arsenic, this effect appeared to be dependent on exposure time.

CELLULAR SITE OF ARSENIC AND CADMIUM

The fractionation of cellular components was determined from the two labeled populations at the end of Experiment I. Approximately half the arsenic was associated with the organic layer surrounding the

TABLE 4. Ambient cadmium concentration, cellular cadmium content, and bioaccumulation ratio (BR) after the initial decrease in growth rate.

Expt	Day of expt	Ambient cadmium concn $\mu g \cdot L^{-1}$	Cellular cadmium content $\mu g\ Cd \cdot (10^9\ \mu m^3)^{-1}$	BR
I	2.8	1.5	0.01	4,220
II	2.0	6.1	0.05	8,910
III	1.9	19.6	0.34	17,000

diatom frustule; nearly 60% of the cadmium, however, was associated with the cell contents (Table 6). These initial studies of the cellular site of arsenic or cadmium have shown that a significant percentage of these trace elements becomes associated with the frustule and its organic coating. More than 80% of sorbed plutonium is also associated with the frustule and its organic coating (unpublished data).

IMPLICATIONS

Increased utilization of fossil fuel in the midwest may result in increasing levels of arsenic and cadmium from their present low ambient concentrations (~2 μg $As \cdot L^{-1}$, Seydel 1972; ≤ 0.1 $\mu g\ Cd \cdot L^{-1}$, Wahlgren et al. 1972). Consequently, ongoing studies of possible adverse effects of these energy-related elements on the delicate structure of the aquatic ecosystem and its individual components are of considerable importance.

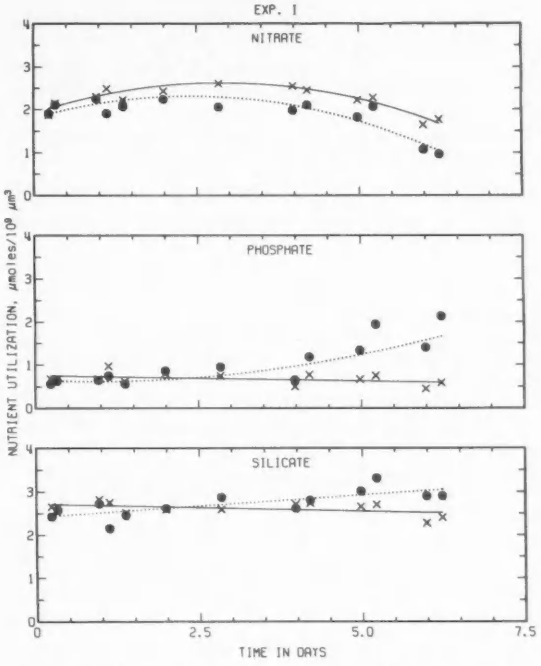

FIG. 8. Micronutrient utilization vs. time for Experiment I: ● for *Asterionella formosa* population exposed to cadmium, and × for control population. Plots for Experiments II and III (not shown) are similar.

TABLE 5. Ratio of the integrated values of micronutrient utilization by the Cd-treated population to that by the control. The values were integrated over the indicated early and late time periods for each of the three experiments.

Expt	Time period (days)	Integrated micronutrient utilization ratio (Cd treated: control) Nitrate	Phosphate	Silicate
I	0.2–4.0	0.9	1.1	1.0
	4.0–6.2	0.8	2.3	1.2
II	0.2–2.0	1.0	1.1	1.0
	2.0–5.0	0.7	1.7	1.1
III	0.1–3.0	1.0	0.8	1.0
	3.0–5.0	1.0	1.4	1.6

TABLE 6. Location of radioactive labels in *Asterionella formosa*.

Fraction	Percent of label ^{74}As	^{115m}Cd
Cell contents	36	58
Organic coating of the frustule	48	25
Siliceous frustule	16	17

The bioaccumulation and recycling dynamics of certain trace elements in the aquatic environment may be closely linked to the regeneration of organic and essential inorganic compounds. Recent studies by Conway et al. (1977) and Parker et al. (1977) have established that between 80 and 100% of the biologically active silicon in Lake Michigan is recycled each year. A similar percentage of the trace elements associated with the frustule may be recycled in conjunction with this biologically active silicon, while the trace elements associated with the organic coating of the frustule and the cellular components may be returned to a dissolved form in conjunction with the recycling of these organic compounds.

Acknowledgments

I thank Dr W. F. Danforth (Illinois Institute of Technology, Chicago) for the inoculum of *Asterionella formosa* and for assistance in formulating synthetic Lake Michigan water; Ms N. L. Peterson (Water Chemistry Laboratory, University of Wisconsin, Madison) for assistance in sampling, data reduction, and the studies to locate the cellular sites of arsenic and cadmium; and Ms E. M. Yaguchi for technical assistance. I also thank Drs J. Alberts, P. Harrison, J. Miller, J. Parker, and F. Throw for their comments on the

manuscript. The work was performed under the auspices of the U.S. Department of Energy.

APPLEBURY, M. E., B. P. JOHNSEN, AND J. E. COLEMAN. 1970. Phosphate binding to alkaline phosphatase. J. Biol. Chem. 245: 4968–4975.

ARMSTRONG, J. A. J., C. R. STEARNS, AND J. D. H. STRICKLAND. 1967. The measurements of upwelling and subsequent biological processes by means of the Technicon AutoAnalyzer® and associated equipment. Deep Sea Res. 14: 381–389.

BUTTON, D. K., S. S. DUNKER, AND M. L. MORSE. 1973. Continuous culture of *Rhodotorula rubra*: Kinetics of phosphate–arsenate uptake, inhibition and phosphate limited growth. J. Bacteriol. 113: 599–611.

CHILDS, C. W. 1971. Chemical equilibrium models for lake water which contains nitrilotriacetate and for "normal" lake water. Proc. 14th Conf. Great Lakes Res. p. 198–210.

CONWAY, H. L. 1977. Interactions of inorganic nitrogen in the uptake and assimilation by marine phytoplankton. Mar. Biol. 39: 221–232.

CONWAY, H. L., AND P. J. HARRISON. 1977. Marine diatoms grown in chemostats under silicate or ammonium limitation. IV. Transient response of *Chaetoceros debilis, Skeletonema costatum* and *Thalassiosira gravida* to a single addition of the limiting nutrient. Mar. Biol. 43: 33–43.

CONWAY, H. L., P. J. HARRISON, AND C. O. DAVIS. 1976. Marine diatoms grown in chemostats under silicate or ammonium limitation. II. Transient response of *Skeletonema costatum* to a single addition of the limiting nutrient. Mar. Biol. 35: 187–199.

CONWAY, H. L., J. I. PARKER, E. M. YAGUCHI, AND D. L. MELLINGER. 1977. Biological utilization and regeneration of silicon in Lake Michigan. J. Fish. Res. Board Can. 34: 537–544.

COPELAND, R. A., AND J. C. AYRES. 1972. Trace element distributions in water, sediment, phytoplankton, zooplankton, and benthos of Lake Michigan: A baseline study with calculations of concentration factors and buildup of radioisotopes in the food web. Environmental Research Group, Ann Arbor, Michigan, ERG Spec. Rep. No. 1: 271 p.

COSSA, D. 1976. Sorption of cadmium by a population of the diatom *Phaeodactylum tricornutum* in culture. Mar. Biol. 34: 163–167.

EICKHORN, G. L., N. A. BERGER, J. J. BUTZOW, P. CLARK, J. M. RIFKIND, Y. A. SHIN, AND E. TARIEN. 1971. The effect of metal ions on the structure of nucleic acids. Am. Chem. Soc., Adv. Chem. Ser. 100: 135–154.

GUILLARD, R. R. L., AND J. H. RYTHER. 1962. Studies of marine planktonic diatoms. I. *Cyclotella nana* (Hustedt) and *Detonula confervacea* (Cleve) Gran. Can. J. Microbiol. 8: 229–239.

HAGER, S. W., L. I. GORDON, AND P. K. PARK. 1968. A practical manual for the use of the Technicon AutoAnalyzer in seawater nutrient analyses. Oregon State Univ., Dep. Oceanogr. Tech. Rep. 68–33: 31 p.

HOLMES, R. W. 1957. Solar radiation, submarine daylight and photosynthesis, p. 109–128. *In* J. W. Hedgpeth [ed.] Treatise on marine ecology and paleoecology. Geol. Soc. Amr. Mem. 67: 109–128.

JUNG, C., AND A. ROTHSTEIN. 1965. Arsenate uptake and release in relation to the inhibition of transport and glycolysis in yeast. Biochem. Pharacol. 14: 1093–1112.

KUBITSCHEK, H. E. 1970. Introduction to research with continuous cultures. Prentice–Hall, Inc., Englewood Cliffs, N.J. 195 p.

LELAND, H. V., E. D. COPERHOVER, AND L. S. CORRILL. 1974. Heavy metals and other trace elements. J. Water Pollut. Control Fed. 46: 1452–1476.

LUNDE, G. 1973. The synthesis of fat and water soluble arseno-organic compounds in marine and limnetic algae. Acta Chem. Scand. 27: 1586–1594.

MILLER, L. R. 1970. Effects of metals on cells, subcellular elements and macromolecules. Charles C. Thomas Publishers, Springfield, Ill. 207 p.

MURPHY, J., AND J. P. RILEY. 1962. A modified single solution method for the determination of phosphate in natural waters. Anal. Chim. Acta 27: 31–36.

O'KELLEY, J. C. 1974. Inorganic nutrients, p. 610–635. *In* W. D. P. Stewart [ed.] Algal physiology and biochemistry. University of California Press, Berkeley, Los Angeles.

PARKER, J. I., H. L. CONWAY, AND E. M. YAGUCHI. 1977. Dissolution of diatom frustules in Lake Michigan. J. Fish. Res. Board Can. 34: 545–551.

SEYDEL, I. S. 1972. Distribution and circulation of arsenic through water, organisms, and sediments of Lake Michigan. Arch. Hydrobiol. 71: 17–30.

SHIAMI, N. T., AND K. W. KUNTZ. 1973. Great Lakes precipitation chemistry. Proc. 16th Conf. Great Lakes Res. p. 581–602.

SILLEN, L. G., AND A. E. MARTELL. 1964. Stability constants of metal-ion complexes. Chem. Soc. Spec. Publ. No. 17: 754 p.

STRICKLAND, J. D. H., AND T. R. PARSONS. 1972. A practical handbook of seawater analysis. Bull. Fish. Res. Board Can. 167: 310 p.

VALLEE, B. L., AND D. D. ULMER. 1972. Biochemical effects of mercury, cadmium and lead. Annu. Rev. Biochem. 41: 91–128.

WAHLGREN, M. A., D. N. EDGINGTON, AND F. F. RAWLINGS. 1972. Determination of selected trace elements in natural water samples using spark source mass spectroscopy. Radiol. Physics Div. Ann. Rep., Environmental Research, January–December 1971, Argonne Natl. Lab. Rep. ANL-7860, Part III: 55–63.

WEILER, R. R., AND V. K. CHAWLA. 1969. Dissolved mineral quality of Great Lakes waters. Proc. 12th Conf. Great Lakes Res. p. 801–818.

WINCHESTER, J. W., AND D. G. NIFONG. 1971. Water pollution in Lake Michigan by trace elements from pollution aerosol fallout. Water, Air, Soil Pollut. 1: 50–64.

Buoyancy Response to Changes in Water Velocity and Its Function in Creek Chub (*Semotilus atromaculatus*)

GORDON BEREZAY AND JOHN H. GEE

Department of Zoology, University of Manitoba, Winnipeg, Man. R3T 2N2

BEREZAY, G., AND J. H. GEE. 1978. Buoyancy response to changes in water velocity and its function in creek chub (*Semotilus atromaculatus*). J. Fish. Res. Board Can. 35: 295–299.

Creek chub (*Semotilus atromaculatus*) reduce buoyancy by decreasing swim-bladder volume when exposed to water current. Fish were near neutral buoyancy (0.956–0.997 $mL \cdot g^{-1}$) in still water but in current small fish (<73 mm) were more buoyant (0.668 $mL \cdot g^{-1}$) than larger fish (0.540 $mL \cdot g^{-1}$). Extent of buoyancy alteration was influenced by acclimation temperature, water velocity, and an interaction of both these factors. Reduction of buoyancy on exposure to water current required 3–6 h and the rate of decrease (0.035–0.068 $mL \cdot g^{-1} \cdot h^{-1}$) was independent of acclimation temperature and water velocity. The hypothesis that creek chub reduce buoyancy when exposed to water current to compensate for the lift created due to deflection of water over the dorsal surface of the body was supported by the following findings. When initially exposed to current, fish lowered the head assuming an angle of attack of 9–12° from horizontal. A horizontal (<1°) angle of attack was gradually assumed during buoyancy adjustment. Fish acclimated to moderate current for 12 or 24 h tired less readily in strong current (80% took 43 and 44 min, respectively) than those not acclimated or acclimated for 6 h (80% took 33 and 25 min, respectively). Fish induced to swim in still water reduced buoyancy to a similar extent as those in current.

Key words: swim-bladder volume change, temperature, hydrodynamic lift, swimming angle of attack, time to fatigue

BEREZAY, G., AND J. H. GEE. 1978. Buoyancy response to changes in water velocity and its function in creek chub (*Semotilus atromaculatus*). J. Fish. Res. Board Can. 35: 295–299.

Les mulets à cornes (*Semotilus atromaculatus*) réduisent leur flottabilité en diminuant le volume de leur vessie gazeuse lorsque exposés à un courant d'eau. Les poissons ont une flottabilité presque neutre (0.956–0.997 $mL \cdot g^{-1}$) en eau morte alors que dans un courant les petits poissons (<73 mm) sont plus légers (0.668 $mL \cdot g^{-1}$) que les poissons plus grands (0.540 $mL \cdot g^{-1}$). La température d'acclimatation, la vitesse du courant et une interaction de ces deux facteurs influencent tous le degré d'altération de la flottabilité. La diminution de flottabilité s'effectue entre 3 et 6 h après exposition à un courant et le taux de diminution (0.035–0.068 $mL \cdot g^{-1} \cdot h^{-1}$) est indépendant de la température d'acclimatation et de la vitesse du courant. Les observations suivantes corroborent l'hypothèse que le mulet à cornes réduit sa flottabilité lorsque exposé à un courant d'eau afin de compenser la poussée causée par la déviation de l'eau sur la surface dorsale du corps. Au début de leur exposition à un courant, les poissons baissent la tête et adoptent un angle d'attaque de 9 à 12° par rapport à l'horizontale. A mesure qu'ils règlent leur flottabilité, ils reprennent un angle d'attaque se rapprochant de l'horizontale (<1°). Les poissons acclimatés à un courant modéré pendant 12 ou 24 h se fatiguent moins rapidement dans un fort courant (80% prennent 43 et 44 min respectivement) que les poissons non acclimatés ou acclimatés pendant 6 h (80% prennent 33 et 25 min respectivement). Les poissons que l'on fait nager dans une eau morte réduisent leur flottabilité au même degré que ceux qu'on expose à un courant.

Received July 8, 1977
Accepted November 30, 1977

Reçu le 8 juillet 1977
Accepté le 30 novembre 1977

WHEN stream fish encounter an increase in water velocity they reduce swim-bladder volume and thus buoyancy. When in still water, the response is reversed and a near-neutral buoyancy is attained (Gee et al. 1974). Factors affecting the rate and extent of buoyancy adjustment remain largely unknown. When tested separately, size of fish, water temperature, and water velocity influence the extent of buoyancy adjustment by fathead minnow, *Pimephales promelas* (Gee 1977) but the effect of interaction between these factors is not clear.

Reasons for buoyancy reduction in current are not fully understood. Alexander (1966) suggested that a reduced buoyancy in current resulted in greater frictional forces between the body of the fish and the substrate, resulting in a substantial saving of energy. This may explain why demersal fish reduce buoyancy in current or have evolved a greatly reduced swim-bladder volume, but it does not explain why fish swimming in

Printed in Canada (J4914)
Imprimé au Canada (J4914)

midwater reduce buoyancy. We propose and provide evidence for our hypothesis that when fish hold a midwater position in current they reduce swim-bladder volume to offset the lift resulting from the airfoil shape of their body. If uncorrected, energy would be required to maintain vertical position and prevent the fish from rising in the water column.

The purpose of this study was to examine the effects of water velocity and temperature on rate of adjustment of buoyancy by creek chub, *Semotilus atromaculatus*, and to relate the size of fish and the interaction of water velocity and temperature to the extent of this buoyancy adjustment.

Materials and Methods

Creek chub were collected from Cypress Creek near Clearwater, Manitoba, between September 24 and November 7, 1975, and held in the laboratory at 12(±1)°C under a photoperiod of 12 h L:12 h D. In all experiments fish were tested in a photoperiod of 14 h L:10 h D. Fish <75 mm long were fed Ewos Salmon Starter (size 3), while larger fish were fed Ewos Trout Starter (size 4P).

Fish were held in either still water or current for specific periods of time to attain maximum and minimum buoyancy, respectively. Current was created in an aquarium (22 × 61 × 61 cm) using the design of Gee and Bartnik (1969). No substrate was used in the swimming chamber and the bottom was opaque plexiglass. Water velocity (up to 85 cm·s^{-1}) was determined by averaging five measurements from different locations, taken 2.5 cm from the bottom with an Ott current meter (Type C1). Still-water conditions were created by holding fish in aquaria (122 × 61 × 61 cm or 90 × 44 × 44 cm) which contained a small gently bubbling airstone.

To determine buoyancy fish were taken by net from either still-water or current aquaria and anesthetized in a solution of MS-222® (ethyl *m*-aminobenzoate methanesulfonate). Fish were not observed to spit gas from their swim-bladder during handling (Berezay 1977). Buoyancy was expressed by dividing the swim-bladder volume (±0.001 mL) by the weight (±0.001 g) of the gas-free fish in water (1.0 mL·g^{-1} = neutral buoyancy). Swim-bladder volume was determined by taking the difference between the weight of the intact fish in water and the weight of the gas-free fish in water. This difference in weight (grams) equals swim-bladder volume (millilitres), as at a given depth a 1-mL volume of gas creates a buoyant lift of 1 g.

Effect of Size, Acclimation Temperature, and Water Velocity

To determine the effect of size of fish on buoyancy attained in still water and current (Experiment 1), three size-groups (58–73, 74–150, 151–224 mm, fork length) of fish were acclimated for 2 wk at 20(±1)°C. Two batches of 10 fish were taken from each size-group. One was held in still water for 72 h and the other in current (35 cm·s^{-1}) for 24 h before buoyancy was measured. Preliminary experiments showed that fish reached minimum buoyancy within 6 h of exposure to current and maintained that level for 8 days (Berezay 1977).

To study the effect of water velocity and acclimation temperature on extent of buoyancy adjustment (Experiment 2) four groups of fish were acclimated for at least 14 days at 6, 12, 20, and 27(±1)°C. At each temperature five batches of seven fish were held at different water velocities (still water, 15, 25, 35, and 45 cm·s^{-1}) and buoyancy was measured after 24 h. At 6 and 12°C fish could not tolerate velocities in excess of 45 cm·s^{-1}.

To determine the effect of acclimation temperature on rate of decrease in buoyancy (Experiment 3), four groups of fish were acclimated for at least 2 wk at 6, 12, 20, and 27(±1)°C. For each group, batches of seven fish were held in still water for at least 3 days and buoyancy measured after either 0, 0.75, 1.5, 3, 6, 12, or 24 h in current (45 cm·s^{-1}).

The effect of different water velocities on rate of buoyancy decrease (Experiment 4) was measured on fish at 20(±1)°C. Groups of fish were held in still water for 3 days and then exposed to water velocities of either 15, 35, 45, 60, or 75 cm·s^{-1}. Buoyancy was measured for batches of seven fish after different periods of time in current (0, 0.75, 1.5, 3, 6, 12, or 24 h).

Why Fish Reduce Buoyancy While Swimming

If a fish is to receive upward lift from its body (apart from using its fins) the shape must be such that there is a greater curve over the dorsal surface than over the ventral. To measure this we traced the lateral outline of the bodies of freshly killed creek chub: four immature fish (112–121 mm fork length), four mature males (183–207 mm), and four ripe females (135–167 mm). A line was drawn through the mouth and the fork of the tail and three points were marked on this line that divided the body from tip of the snout to the caudal peduncle into four equidistant sections. At each point the width of the dorsal and ventral portions of the body was measured. The latter was divided into the former and the average of the three was calculated for each fish.

If the hypothesis that fish reduce buoyancy while swimming in midwater to compensate for the increased lift from the body is correct, then one would suspect the following:

1. Prior to completion of buoyancy adjustment fish would compensate by altering the horizontal axis of the body (swimming angle of attack).
2. In strong current fish at non-optimal buoyancy would fatigue more quickly than those at optimal buoyancy.
3. Fish forced to swim in still water would reduce buoyancy.

The swimming angle of attack was measured on creek chub following exposure to current (Experiment 5). An aspect meter mounted on a tripod (Berezay 1977) was used to measure the difference in angle between the horizontal axis of the fish (tip of snout to fork of tail) and the axis of the water flow. Six fish were acclimated for 14 days at 12(±1)°C in still water. Swimming angle of attack was measured for fish exposed to current (45 cm·s^{-1}) after 0, 0.25, 0.5, 0.75, 1, 1.5, 3, and 6 h.

To determine whether fish tired more quickly in current when not at the correct buoyancy (Experiment 6), a group of fish was acclimated for at least 14 days at 12(±1)°C. Four batches of 10 fish were held in either still water for 72 h or current (45 cm·s^{-1}) for either 6, 12, or 24 h prior to exposure to strong current (80 cm·s^{-1}). Time to fatigue was measured for each fish. It was expressed as the time exposed to strong current until the fish was unable to maintain position and rested against the outlet screen of the current chamber for 90 s.

To determine the effect of swimming in still water on

buoyancy (Experiment 7) a group of fish was acclimated at 20(±1)°C under a 12-h photoperiod for 14 days. A batch of seven fish was induced to swim at a mean speed of 15 cm·s^{-1} in an optomotor response system (Berezay 1977) for 0.75 h and their buoyancy determined. Still-water buoyancy was determined for another batch of seven fish.

Results

Effect of Size, Acclimation Temperature, and Water Velocity

Experiment 1 — Buoyancy did not vary significantly between size-groups in still water and fish were at a near-neutral buoyancy. In current, fish in the two larger size-groups showed similar decreases in buoyancy, which were significantly ($P \leq 0.05$; analysis of variance) greater than that of the smallest size-group, shown as follows:

Fork length (mm)	58–73	74–150	151–224
Mean buoyancy (mL·g^{-1}, n=10)			
Still	0.983	0.971	0.986
Current	0.668	0.546	0.533

Experiment 2 — The effects on buoyancy of water velocity, temperature, and their interaction were significant ($P < 0.05$; two-way analysis of variance). At 6 and 12°C buoyancy attained diminished with increasing water velocity and the lowest buoyancy was achieved at the fastest water velocity (45 cm·s^{-1}; Fig. 1). At 20 and 27°C the lowest buoyancy was attained at 25 cm·s^{-1}, and at 20°C similar values were recorded at faster velocities, but at 27°C buoyancy increased significantly ($P \leq 0.05$; Student–Newman–Keuls test) from 25 to 45 cm·s^{-1} (Fig. 1).

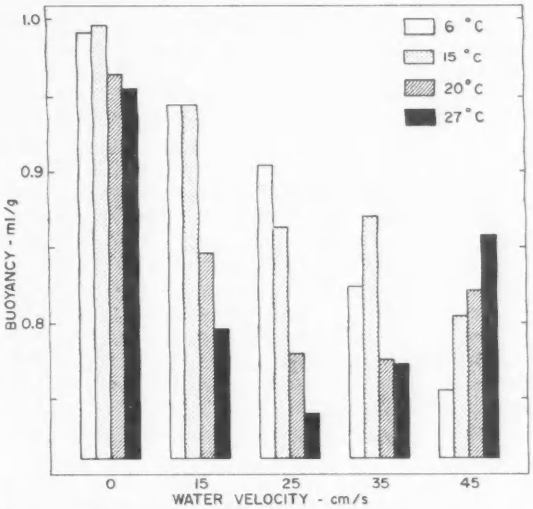

Fig. 1. Effect of acclimation temperature and water velocity on buoyancy response.

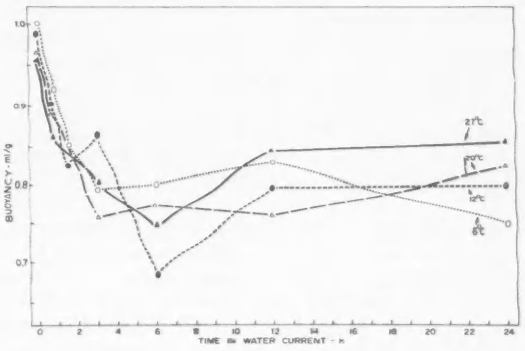

Fig. 2. Effect of acclimation temperature on rate of decrease in buoyancy.

Experiment 3 — Fish reduced buoyancy at similar rates ($P > 0.05$; analysis of covariance) when exposed to current for 6 h at different acclimation temperatures, shown as follows:

Acclimation temp (°C)	6	12	20	27
Slope of regression line (buoyancy against time)	−0.00053	−0.00074	−0.00050	−0.00049

Differences between mean buoyancy values attained following 6 h in current at 6 and 20°C were not significant, but at 12 and 27°C fish increased buoyancy significantly ($P < 0.05$; analysis of variance) between 6 and 24 h in current (Fig. 2).

Experiment 4 — When exposed to water velocity, fish reduced buoyancy, reaching a minimum within 6 h independent of water velocity, as slopes of regression lines calculated for each velocity were similar ($P > 0.05$; analysis of covariance), shown as follows:

Water velocity (cm·s^{-1})	15	35	45	60	75
Slope of regression line (buoyancy against time)	−0.00030	−0.00048	−0.00048	−0.00050	−0.00051

Why Fish Reduce Buoyancy

The curve of the dorsal surface of creek chub exceeds that of the ventral surface (width of dorsal portion > width of ventral portion). The exception being that when females are gravid the curves become similar. The mean width of the dorsal portion of the body divided by that of the ventral portion for individual

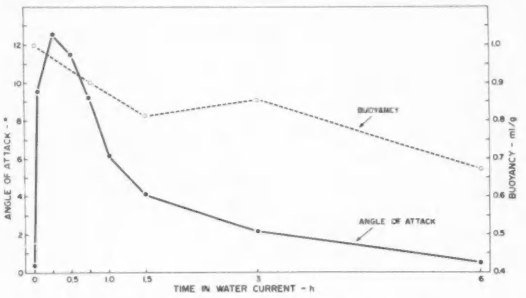

FIG. 3. Relationship between angle of attack and buoyancy after exposure to current.

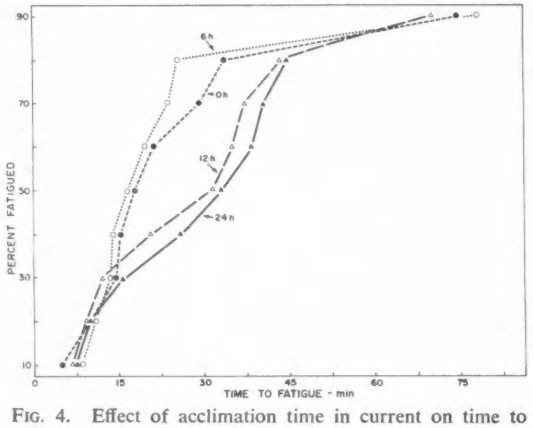

FIG. 4. Effect of acclimation time in current on time to fatigue.

chub were as follows (means for each group in parentheses):

Immature chub	1.5	1.4	1.1	1.2	(1.3)
Mature males	1.2	1.2	1.5	1.1	(1.3)
Gravid females	1.2	0.9	1.1	0.8	(1.0)

Experiment 5 — When fish acclimated to still water initially encountered current (45 cm·s^{-1}), they showed an angle of attack in which the horizontal body axis was 9–12° from the horizontal axis of the water flow (head lowered). This was reduced over time as buoyancy was reduced (Fig. 3). After 6 h in current, when buoyancy response was stabilized, the angle of attack was reduced to $\leq 1°$ (horizontal axis of fish is almost parallel to current flow). These fish were visibly able to compensate more easily for turbulent fluctuations in the current and appeared to have decreased the frequency of their tail beats.

Experiment 6 — Fish acclimated to moderate current (45 cm·s^{-1}) for 0 to 6 h became fatigued more quickly in strong current (80 cm·s^{-1}) than those fish acclimated for 12 or 24 h (Fig. 4). In the former, 80% of the fish tired within 34-min exposure to strong current, while the latter required 44 min before 80% of the fish were fatigued. Regression lines were calculated for the number of fish fatigued (up to eight) over time in the four periods of acclimation to current and were as follows:

$$\begin{aligned} 0\text{ h};\ y &= -1.60 + 0.042x, \\ 6\text{ h};\ y &= -19.66 + 0.065x, \\ 12\text{ h};\ y &= 2.86 + 0.028x, \\ 24\text{ h};\ y &= 1.16 + 0.027x. \end{aligned}$$

Differences between slopes were significant ($P < 0.05$; analysis of covariance). Acclimation time in current (45 cm·s^{-1}), and thus buoyancy, affect swimming efficiency or time to fatigue in strong current.

Experiment 7 — When induced to swim at 15 cm·s^{-1} in still water, fish reduced buoyancy significantly ($P < 0.05$; one-way analysis of variance). Extent of buoyancy adjustment in the optomotor tank and that in the current aquarium were similar with mean buoyancy values (millilitres per gram) shown as follows:

Optomotor tank	
Resting	0.954
Induced to swim (45 min)	0.902
Current aquarium	
Still water	0.964
Current (45 min)	0.865

Discussion

Effect of Size, Acclimation Temperature, and Water Velocity

The size-dependent difference in the range over which buoyancy is adjusted relate well to the water velocities encountered by creek chub in nature. Immature fish (>81 mm) are most abundant in large pools of streams and rivers where water velocity is least, even at peak flows. But larger fish spawn over a 2-wk period in May, at temperatures between 10 and 20°C and in water velocities from 15 to 45 cm·s^{-1} (Moshenko and Gee 1973). Within these ranges of temperature and water velocity creek chub could adjust to the minimum buoyancy level (Experiment 2), facilitating maintenance of territorial position in current and thus enhancing reproductive success.

The interaction of temperature and water velocity allow creek chub to adjust buoyancy to meet particular combinations of these variables. But the rate at which creek chub reduce buoyancy to meet these changes is independent of temperature and water velocity (Experiments 3 and 4). This would be advantageous in an environment where extremes of both factors are encountered often and occur independently from one another.

Creek chub may be unable to maintain a minimum buoyancy longer than a few hours when acclimated to high temperatures and exposed to fast water velocities. Fish acclimated to 27°C and held for 24 h in a water

velocity of 45 cm·s^{-1} had a significantly higher buoyancy than those held in velocities of 25 or 35 cm·s^{-1} (Experiment 2). This increase in buoyancy with higher velocities is explained by Experiment 3, which showed that fish acclimated to 27°C in still water and then exposed to a velocity of 45 cm·s^{-1} reached a minimum buoyancy by 6 h after exposure to current but that by 12 and 24 h after exposure buoyancy had increased significantly. At 27°C creek chub are near their upper incipient lethal temperature (30.3°C; Hart 1952) and this combined with a fast velocity could have produced stress on the fish, affecting swim-bladder volume and the resulting buoyancy. The effects of environmental stress on rate and extent of swim-bladder alteration and the ability to maintain a particular buoyancy remain unknown.

Why Fish Reduce Buoyancy

Various lines of argument support the hypothesis that lift due to swim-bladder volume is reduced to compensate for increased lift from the body shape as increased water velocity is encountered.

First, the extent of buoyancy reduction increases as water velocity increases in a number of species including juvenile Atlantic salmon (Neave et al. 1966), fathead minnows (Gee 1977), and rainbow trout (J. H. Gee unpublished data), as well as in creek chub. Lift from the body shape would be greater at higher water velocities, requiring greater reduction in lift from the swim bladder.

Second, creek chub require 3–6 h to reduce buoyancy to the minimum sustained buoyancy level (Experiments 3 and 4). To compensate for the excess lift during the time buoyancy is adjusted, the swimming angle of attack is lowered as current is initially encountered. The body of the fish gradually approaches a horizontal position as buoyancy is adjusted (Experiment 5). This initial correction for excess lift is very inefficient, as drag would be greatly increased, a factor that would favor a rapid reduction in buoyancy so that the fish can attain maximum benefit from its streamlined body shape.

Third, fish at or near neutral buoyancy are less tolerant of fast water velocities than those that have a reduced buoyancy (Experiment 6). Fish that were not acclimated to current or were acclimated for only 6 h tired more quickly than those acclimated to current for either 12 or 24 h. At 6 h fish have adjusted buoyancy but still appear to be intolerant of current. This may be due to stress encountered while adjusting buoyancy, resulting in the formation of lactic acid, which is removed very slowly from the body tissues (Black et al. 1959).

Fourth, fish swimming in still water would generate similar lift forces to those holding position in current (Experiment 7). These fish reduced buoyancy, suggesting that body shape does create lift.

Finally, indirect evidence supporting the hypothesis was observed in the northern pike (*Esox lucius*), which increased buoyancy when exposed to current (Gee et al. 1974). The largest portion of the body is below midline, with a flat back, converse to that of the creek chub. Deflection of water around its body would create a downward force rather than an upward force, requiring an increase in swim-bladder volume to maintain the equilibrium between lift and weight in water.

In conclusion, water velocity and temperature interact to determine a specific buoyancy level, although neither factor affects the rate of decrease in buoyancy as current is encountered. The hypothesis that creek chub reduce buoyancy in water velocity to overcome the lift produced by the hydrofoil shape of their body is substantiated.

Acknowledgments

This research was supported by grants from the Northern Studies Committee of the University of Manitoba and the National Research Council of Canada. We thank Dr E. Scherer and Mr S. Nowak for making available the optomotor equipment. Drs T. J. Wiens, K. W. Stewart, E. Scherer, and S. K. Sen provided helpful comments on the preparation of the manuscript.

Alexander, R. McN. 1966. Physical aspects of swimbladder function. Biol. Rev. (Cambridge) 41: 141–176.

Berezay, G. 1977. Buoyancy response to water velocity by creek chub (*Semotilus atromaculatus*) and its function. M.Sc. Thesis. Univ. Manitoba, Winnipeg, Man. 46 p.

Black, E. E., W. G. Chi, F. D. Forbes, and A. Hanslip. 1959. Changes in pH, carbonate and lactae of the blood of yearling trout, *Salmo gairdneri*, during and following severe muscular activity. J. Fish. Res. Board Can. 16: 391–402.

Gee, J. H. 1977. Effects of size of fish, water temperature and water velocity on buoyancy alteration by fathead minnows, *Pimephales promelas*. Comp. Biochem. Physiol. 65A: 503–508.

Gee, J. H., and V. G. Bartnik. 1969. Simple stream tank simulating a rapids environment. J. Fish. Res. Board Can. 26: 2227–2230.

Gee, J. H., K. Machniak, and S. M. Chalanchuk. 1974. Adjustment of buoyancy and excess internal pressure of swimbladder gases in some North American freshwater fishes. J. Fish. Res. Board Can. 31: 1139–1141.

Hart, J. S. 1952. Geographic variations of some physiological and morphological characters in certain freshwater fish. University of Toronto Press, Toronto. Biol. Ser. No. 60: 11–79.

Moshenko, R. W., and J. H. Gee. 1973. Diet, time and place of spawning and environment occupied by creek chub (*Semotilus atromaculatus*) in the Mink River, Manitoba. J. Fish. Res. Board Can. 30: 357–362.

Neave, N. M., C. L. Dilworth, J. G. Eales, and R. L. Saunders. 1966. Adjustment of buoyancy in Atlantic salmon parr in relation to changing water velocity. J. Fish. Res. Board Can. 23: 1617–1620.

Applicability of Phosphorus Budget Models to Small Precambrian Lakes, Algonquin Park, Ontario

W. A. SCHEIDER[1]

Department of Zoology, University of Toronto, Toronto, Ont. M9W 5L1

SCHEIDER, W. A. 1978. Applicability of phosphorus budget models to small Precambrian lakes, Algonquin Park, Ontario. J. Fish. Res. Board Can. 35: 300–304.

Phosphorus and hydrological budgets were constructed for four small lakes with Precambrian drainage in Algonquin Park, Ontario. Lake outflow discharge ranged from 21.7×10^5 to 177×10^5 $m^3 \cdot yr^{-1}$. Annual phosphorus input to the lakes from terrestrial drainage and precipitation totaled 36.3–188 $kg \cdot yr^{-1}$. The lakes retained 16–41% of the annual input. These data were used to test a series of models that predict the spring total phosphorus concentration in lake water and the mean summer chlorophyll *a*. The predicted spring phosphorus concentration agreed well with measured values (within 1.3 $mg \cdot m^{-3}$) except where human-associated phosphorus input may have contributed to the phosphorus budget of the lake. Agreement between predicted and measured chlorophyll *a* was not as close. A figure of 0.48 kg $P \cdot capita^{-1} \cdot yr^{-1}$ was calculated as the human-associated supply.

Key words: phosphorus budget, chlorophyll *a*, predictive model, Precambrian lake

SCHEIDER, W. A. 1978. Applicability of phosphorus budget models to small Precambrian lakes, Algonquin Park, Ontario. J. Fish. Res. Board Can. 35: 300–304.

Nous avons établi les budgets de phosphore et les budgets hydrologiques de quatre petits lacs à bassins hydrographiques précambriens du parc Algonquin en Ontario. Le débit des effluents de ces lacs varie de 21.7×10^5 à 177×10^5 $m^3 \cdot an^{-1}$. Les apports annuels de phosphore dans ces lacs provenant du ruissellement et de la précipitation sont au total de 36.3 à 188 $kg \cdot an^{-1}$. Les lacs retiennent de 16 à 41% des apports annuels. Utilisant ces données, nous avons vérifié une série de modèles permettant de prédire la concentration vernale de phosphore total dans l'eau des lacs et la concentration estivale moyenne de chlorophylle *a*. La concentration de phosphore prédite pour le printemps s'accorde bien avec les valeurs mesurées (marge de 1.3 $mg \cdot m^{-3}$), sauf dans les cas où des apports de phosphore liés aux activités humaines peuvent avoir contribué au budget de phosphore du lac. Dans le cas de la chlorophylle *a*, les valeurs prédites ne s'accordent pas aussi bien avec les valeurs mesurées. On calcule que l'apport associé aux activités humaines est de 0.48 kg $P \cdot tête^{-1} \cdot an^{-1}$.

Received September 22, 1977
Accepted December 2, 1977

Reçu le 22 septembre 1977
Accepté le 2 décembre 1977

DILLON and Rigler (1974a, b) proposed a series of models to predict the phosphorus concentration in lake water at spring turnover and the mean summer concentration of chlorophyll *a*, a measure of algal abundance. The schemes are a combination of Vollenweider's (1969) model for the chemical budget of an oligotrophic lake and the relationship between phosphorus and chlorophyll *a* first published by Sakamoto (1966). In its simplest version, the phosphorus budget model was expressed by Scheider (1974) as

$$[P] = \frac{J\,(1 - R)}{Q} \quad (1)$$

The variables necessary to test the model are the concentration of total phosphorus at spring turnover ([P] in grams per cubic metre), the total annual supply of phosphorus to the lake from terrestrial and atmospheric sources (J in grams per year), the percent of incoming phosphorus retained annually by the lake (R), and the total annual lake outflow discharge (Q in cubic metres per year).

Although already useful for water quality management (Dillon and Rigler 1975), the models have not been tested against many types of lakes and their confidence limits for prediction are wide. The purpose of my work was to test the applicability of the Dillon–Rigler method to lakes with surface areas (0.13–0.41 km^2) smaller than those already tested. Rigler (1956) demonstrated that in small lakes strong pelagial–littoral interactions can affect the phosphorus concentration in surface waters. Thus, small lakes, which may exhibit greater changes in total phosphorus concentrations throughout the year, cannot be expected a priori to fit the model as well as large lakes.

Data collected to test the Dillon–Rigler method was also applied to other models that predict terrestrial unit

[1]Present address: Ontario Ministry of the Environment, Water Resources Branch, Limnology and Toxicity Section, Rexdale, Ont. M9W 5L1.

Printed in Canada (J4991)
Imprimé au Canada (J4991)

TABLE 1. Latitude, longitude, lake surface area (A_o), mean depth ($\bar{z}$), lake volume (V), drainage basin area (A_D), total dissolved solids (TDS), total alkalinity, and total nitrogen (N) to total phosphorus (P) ratios for the study lakes.

Lake	Lat. (°N)	Long. (°W)	A_o (km²)	$\bar{z}$ (m)	V ($m^3 \times 10^6$)	A_D[a] (km²)	TDS[b] ($mg \cdot L^{-1}$)	Alkalinity[b] ($mg \cdot L^{-1} CaCO_3$)	N:P[c]
Brewer	45°35′	78°20′	0.41	5.7	2.30	4.26	46	8.0	26
Costello	45°35′	78°20′	0.34	8.4	2.89	11.47	43	8.7	44
Kearney	45°34′	78°25′	0.32	7.3	2.33	17.03	34	8.3	24
Clarke	45°32′	78°16′	0.20	5.6	1.12	33.29	—	—	28
Little McCauley	45°35′	78°18′	0.18	3.8	0.69	2.38	33	7.3	36
Found	45°33′	78°39′	0.13	11.6	1.50	0.18	—	—	—

[a]Drainage basin area excludes lake surface area.
[b]3-yr means taken in July (R. A. Ryder personal communication).
[c]5-yr spring means (R. R. Langford personal communication).

runoff (Pentland 1968; Morton 1976), terrestrial phosphorus export (Dillon and Kirchner 1975), and phosphorus retention by lakes (summarized in Larsen and Mercier 1976).

Study Area

The six lakes studied lie in Algonquin Park on forested Precambrian shield plutonic bedrock. Logging activity is minimal or nonexistent in the watersheds as is permanent human habitation. A campground on the southeast shore of Kearney Lake is used in the summer.

Location, morphometry, and drainage basin areas of the lakes as well as some chemical background data are given in Table 1. Comparison with Ryder (1964) shows the lake total dissolved solids (TDS) and alkalinity values to be typical of those in the area. The spring nitrogen–phosphorus ratios are >12, falling between 24 and 44, indicating that phosphorus is probably the element in shortest supply (Sakamoto 1966).

Materials and Methods

Phosphorus budgets were constructed on four lakes: Brewer, Kearney, Clarke, and Costello. The phosphorus–chlorophyll *a* relationship was tested on an additional two lakes: Found and Little McCauley.

Lakes were echo sounded with a Furuno Model FG-200 Mark 3 and morphometric data calculated after Hutchinson (1957). Data are given by Scheider (1974). Drainage basin areas were delineated by stereoscopic study of aerial photographs following the high points of land. Areas were calculated by planimetry.

Relevant data on stream discharge and phosphorus concentrations taken from 1953 to 1956 existed on three of the six lakes under study (R. R. Landford unpublished data). As differences in analytical methods can affect results, a comparison of 1953–56 versus 1973 phosphorus concentrations was carried out to check the validity of the figures.

Discharge for 12 streams was measured with 90° V-notch and rectangular weirs; current meter measurements were taken at 20 and 80% of water depth across a surveyed section of stream and dye dilution. Measurements for most streams were made 1–3 times weekly. Areas of miscellaneous drainage (areas with no clearly defined or gaugeable streams) were small for three lakes, ranging from 6 to 20% of the total drainage basin area. The exception was Brewer Lake, with 41% of the basin as miscellaneous drainage. For these areas monthly runoff figures given by Pentland (1968) were used to calculate discharge. Pentland's figures were checked against measured values on gauged streams, and correction factors applied to the ungauged areas where necessary. To obtain a figure for phosphorus export, the mean export value for the measured streams was applied to the miscellaneous drainage areas. Streams were sampled from shore with widemouthed polyethylene bottles and triplicate subsamples pipetted immediately into Erlenmeyer flasks. The water was eventually digested and analyzed for total phosphorus in these same flasks.

Two sets of samples of lake water from two locations per lake were collected within 3 wk of ice melt in the spring of 1973. A polyethylene tube was lowered to within 1 m of bottom to obtain a column sample of water. Triplicate subsamples were taken from the pooled sample. Concurrent temperature profiles showed the lakes to be thermally homogeneous for the sampling periods.

Two rain collectors were positioned on rafts and one onshore to sample phosphorus in precipitation from May to September 1973. Collectors were rinsed before and after each rainfall with dilute nitric acid and distilled water; thus only the phosphorus in wet fallout was monitored.

Studies in the same area by Dillon (1974) and Schindler and Nighswander (1970) give phosphorus loading in bulk and wet fallout, respectively. Bulk precipitation is that collected in a continuously open vessel. Dry fallout is the difference between bulk and wet. A summer bulk to wet loading ratio (2.2:1) was calculated from these studies and applied to my figures to correct for dry fallout. The summer figure was not extrapolated to an annual load because precipitation loadings are greater in summer than winter (Kluesner 1972; Dillon 1974; Schindler and Nighswander 1970; Allen et al. 1968). Values from forested areas of the Canadian Shield similar to the study area were used to estimate winter phosphorus load (Barica and Armstrong 1971; Dillon 1974; Schindler and Nighswander 1970).

Analyses for total phosphorus were done after Strickland and Parsons (1968) with the modifications of Dillon (1974). Phosphorus samples taken from 1953 to 1956 were digested with perchloric acid and analyzed colorimetrically by a phosphomolybdate technique.

Lakes were sampled weekly at two deep-water locations through twice the Secchi disc depth for chlorophyll analyses. The method described by UNESCO (1966) with the modifications of Dillon (1974) was used to determine chlorophyll *a* content.

TABLE 2. Comparison of 1953–56 and 1973 stream phosphorus concentrations (May–August). Number of samples in parentheses.

Stream	Mean value ($mg \cdot m^{-3}$) 1953–56	1973
Kearney NW Inlet	14.54 (40)	13.48 (16)
Kearney NE Inlet	21.12 (29)	24.06 (10)
Costello Outflow	6.94 (40)	8.27 (32)
Brewer Outflow	12.50 (23)	8.51 (32)

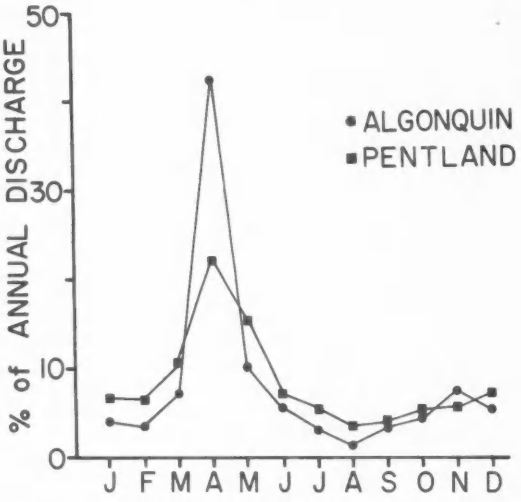

FIG. 1. Predicted (Pentland 1968) and measured (mean value of six Algonquin streams) percent of annual discharge occurring in each month.

Results and Discussion

Data on stream phosphorus concentrations taken in 1953–56 were pooled with those taken in 1973 because statistical analysis by *t*-test showed no significant difference ($\alpha = 0.05$) in three of the four streams compared (Table 2).

The mean annual 1953–56 measured runoff was compared with the runoff predicted from precipitation minus evapotranspiration (Morton 1976) and from the unit runoff model of Pentland (1968). For six streams tested, mean measured areal unit runoff was $0.31\ m \cdot yr^{-1}$. Pentland (1968) found unit runoff $= 0.43\ m \cdot yr^{-1}$ for the same area and calculation of precipitation minus evapotranspiration yields a unit runoff of $0.38\ m \cdot yr^{-1}$. The differences in values occurred despite the similarity of long-term mean annual rainfall (86.4 cm) and 1953–56 mean annual rainfall (90.4 cm). Also, comparison of the measured and predicted (Pentland 1968) percent of annual discharge occurring in each month (Fig. 1) showed measured values rising to a higher peak in April and generally remaining lower than Pentland's values for the remainder of the year. The presence of lakes and control dams in the larger basins employed by Pentland probably acted to dampen peak flow. These results indicate that runoff models should be applied with caution and used only as approximations.

TABLE 3. Terrestrial phosphorus export per unit drainage basin area in eight streams studied.

Stream	Drainage area (km^2)	Annual phosphorus export ($mg \cdot m^{-2} \cdot yr^{-1}$)
Kearney NW	10.04	3.91
Kearney NE	3.48	2.72
Kearney No. 3	2.30	2.43
Brewer No. 1	1.83	7.56
Clarke N	27.86	5.58
Clarke S	3.33	5.28
Costello No. 1	3.36	4.07
Costello No. 4	1.10	4.32

Values for the terrestrial export of phosphorus per unit drainage basin area are summarized in Table 3. The mean value for the eight inflowing streams monitored is $4.5\ mg \cdot m^{-2} \cdot yr^{-1}$ with a range of 2.4–7.6 $mg \cdot m^{-2} \cdot yr^{-1}$. This compares well with Dillon and Kirchner (1975), who reported a mean phosphorus export of $4.7\ mg \cdot m^{-2} \cdot yr^{-1}$ and a range of 0.7–8.8 $mg \cdot m^{-2} \cdot yr^{-1}$ for plutonic–igneous forested watersheds.

Bulk phosphorus loading via precipitation was estimated to be $35\ mg \cdot m^{-2} \cdot yr^{-1}$, falling within the range of reported values for forested areas on the Canadian Shield. Other values are $77.2\ mg \cdot m^{-2} \cdot yr^{-1}$ (Dillon 1974), $37\ mg \cdot m^{-2} \cdot yr^{-1}$ (Gomolka 1975), and $74.4\ mg \cdot m^{-2} \cdot yr^{-1}$ (Nicholls and Cox 1977). Schindler and Nighswander (1970) report $35\ mg \cdot m^{-2} \cdot yr^{-1}$ in wet fallout only. Schindler et al. (1976) report phosphorus loadings of 24–53 $mg \cdot m^{-2} \cdot yr^{-1}$ in northwestern Ontario. In my study, the phosphorus loading in precipitation ranged from 4% of the total load in Clarke Lake to 40% in Brewer Lake. This reaffirms the potential importance of atmospheric contributions, especially in lakes with small drainage basin area to lake surface area ratios.

Retention of phosphorus by the lake is measured as

$$R = \frac{J - Q\,[P_o]}{J}, \tag{2}$$

where $[P_o]$ is phosphorus concentration in the lake outflow. Larsen and Mercier (1976) presented five relationships between retention (R_p), flushing rate (ρ), and areal water load ($q_s = Q/A_o$). The equation that best predicted retention in my lakes was $R_p = 1/1 \times \rho^{0.5}$ (regressing measured on predicted retention $r = 0.93$, $n = 4$).

The variables necessary to construct the hydrologic and phosphorus budgets of four lakes are summarized in Table 4. The range of variables is large for the small number of lakes involved, providing a fairly rigorous

TABLE 4. Total annual phosphorus supply (J), phosphorus retention (R), and lake outflow discharge (Q) in four study lakes.

Lake	J ($kg \cdot yr^{-1}$)	R	Q ($m^3 \cdot yr^{-1} \times 10^5$)
Brewer	36.3	0.41	21.7
Costello	63.3	0.47	34.0
Kearney	70.7	0.28	53.7
Clarke	188.0	0.16	177.0

TABLE 5. Predicted (Scheider 1974) and measured lake-water phosphorus concentrations and predicted (Dillon and Rigler 1974b) and measured mean summer chlorophyll a concentrations.

Lake	Measured [P] ($mg \cdot m^{-3}$)	Predicted [P] ($mg \cdot m^{-3}$)	Measured [chl a] ($mg \cdot m^{-3}$)	Predicted [chl a] ($mg \cdot m^{-3}$)
Brewer	8.60	9.87	3.0	1.8
Costello	9.58	9.87	3.9	2.1
Kearney	12.1	9.48	2.6	2.9
Clarke	10.0	8.92	3.1	2.2
Found	6.98	—	1.1	1.3
Little McCauley	7.09	—	3.3	1.4

test of the models. Lake outflow discharge varies from 21.7×10^5 to 177×10^5 $m^3 \cdot yr^{-1}$, phosphorus supply from 36.3 to 188 $kg \cdot yr^{-1}$, and retention from 0.47 to 0.16. In these four lakes, the predicted (Dillon and Rigler 1974a; Scheider 1974) spring phosphorus concentrations differed from the measured values by 3–22%. Based on this small sample size, the Dillon–Rigler (1974a) phosphorus budget models apparently have good predictive value for small Precambrian lakes.

The greatest difference between measured [P] and predicted [P] (Table 5) occurred in Kearney Lake. This is the only lake with a significant amount of human habitation (campground) in its drainage basin. By assuming that the difference between measured and predicted phosphorus concentrations was due solely to phosphorus supplied from human activities, the per capita phosphorus input can be estimated. The calculated total phosphorus supply ($J = [P]\,Q/1 - R$) necessary to give a measured lake water [P] of 12.1 $mg \cdot m^{-3}$ is 90.3 $kg \cdot yr^{-1}$. The measured natural supply is 70.7 $kg \cdot yr^{-1}$ and thus by difference, 19.6 $kg \cdot yr^{-1}$ is the human-associated input. User statistics for the Kearney campsite (1976) are 40.6 capita $years \cdot yr^{-1}$ (Park Management Branch, Ontario Ministry of Natural Resources, personal communication). Thus, 0.48 $kg \cdot capita^{-1} \cdot yr^{-1}$ is the estimated supply of phosphorus from human-associated activities. Johnson and Owen (1971) found a mean of 2.0 $kg \cdot capita^{-1} \cdot yr^{-1}$ from six municipalities in the Bay of Quinte watershed. Dillon and Rigler (1975) reported 0.8 $kg \cdot capita^{-1} \cdot yr^{-1}$ as the mean value of 13 studies dealing with domestic sewage in Europe and North America. My value is lower because it applies to a recreational setting and usage of the campsite is seasonal.

Agreement between predicted (Dillon and Rigler 1974b) and measured chlorophyll a values (Table 5) for six lakes tested was not as close (12–58%). Although all measured values fell within the 95% confidence limits for prediction (Dillon and Rigler 1974b), the correlation coefficient between $\log_{10}$ [P] and $\log_{10}$ [chl a] was only 0.39.

In conclusion, the Dillon–Rigler (1974a) phosphorus budget model has good predictive value in small Precambrian lakes in spite of possible pelagial–littoral interactions affecting surface-water phosphorus concentrations. The phosphorus–chlorophyll a relation (Dillon–Rigler 1974b) had weaker predictive value.

Acknowledgments

I express my gratitude to Dr F. H. Rigler and Dr R. R. Langford for their help throughout this study. W. G. Coombs ably assisted in the field. Dr F. H. Rigler and G. L. Beggs critically commented on the manuscript.

ALLEN, S. E., A. CARLISLE, E. J. WHITE, AND C. C. EVANS. 1968. The plant nutrient content of rainwater. J. Ecol. 56: 497–504.

BARICA, J., AND F. A. J. ARMSTRONG. 1971. Contribution by snow to the nutrient budget of small northwest Ontario lakes. Limnol. Oceanogr. 16: 891–899.

DILLON, P. J. 1974. The prediction of phosphorus and chlorophyll concentrations in lakes. Ph.D. Thesis. Univ. of Toronto, Toronto, Ont. 330 p.

DILLON, P. J., AND W. B. KIRCHNER. 1975. The effects of geology and land use on the export of phosphorus from watersheds. Water Res. 9: 135–148.

DILLON, P. J., AND F. H. RIGLER. 1974a. A test of a simple nutrient budget model predicting the phosphorus concentration in lake water. J. Fish. Res. Board Can. 31: 1771–1778.

1974b. The phosphorus–chlorophyll relationship in lakes. Limnol. Oceanogr. 19: 767–773.

1975. A simple method for predicting the capacity of a lake for development based on lake trophic status. J. Fish. Res. Board Can. 32: 1519–1531.

GOMOLKA, R. E. 1975. An investigation of atmospheric phosphorus as a source of lake nutrient. M.Sc. Thesis. Univ. of Toronto, Toronto, Ont. 167 p.

HUTCHINSON, G. E. 1957. A treatise on limnology. Vol. 1. John Wiley and Sons, Inc., New York, N.Y.

JOHNSON, M. G., AND G. E. OWEN. 1971. Nutrients and nutrient budgets in the Bay of Quinte, Lake Ontario. J. Water Pollut. Control Fed. 43: 836–853.

KLUESNER, J. W. 1972. Nutrient transport and transformations in Lake Wingra, Wisconsin. Ph.D. Thesis. Univ. of Wisconsin. 181 p.

LANGFORD, R. R. 1950. Fertilization of lakes in Algonquin Park, Ontario. Trans. Am. Fish. Soc. 78: 133–144.

LARSEN, D. P., AND H. T. MERCIER. 1976. Phosphorus retention capacity of lakes. J. Fish. Res. Board Can. 33: 1742–1750.

MORTON, F. I. 1976. Climatological estimates of evapotranspiration. J. of Hydraulics Div., Proc. Am. Soc. Civ. Eng. 102: 275–291.

NICHOLLS, K. H., AND C. M. COX. 1977. Atmospheric nitrogen and phosphorus loading to Harp Lake, Ontario, Canada. Ontario Ministry of the Environment. 12 p.

PENTLAND, R. L. 1968. Runoff characteristics in the Great Lakes basin. Proc. 11th Conf. Great Lakes Res. Int. Assoc. Great Lakes Res. p. 326–359.

RIGLER, F. H. 1956. A tracer study of the phosphorus cycle in lakewater. Ecology 37: 550–562.

RYDER, R. A. 1964. Chemical characteristics of Ontario lakes as related to glacial history. Trans. Am. Fish. Soc. 93: 260–268.

SAKAMOTO, M. 1966. Primary production of phytoplankton community in some Japanese lakes and its dependence on lake depth. Arch. Hydrobiol. 62: 1–68.

SCHEIDER, W. A. 1974. The prediction of phosphorus and chlorophyll concentrations in small shield lakes. M.Sc. Thesis. Univ. of Toronto, Toronto, Ont. 129 p.

SCHINDLER, D. W., R. W. NEWBURY, K. G. BEATY, AND P. CAMPBELL. 1976. Natural water and chemical budgets for a small Precambrian lake in central Canada. J. Fish. Res. Board Can. 33: 2526–2543.

SCHINDLER, D. W., J. E. NIGHSWANDER. 1970. Nutrient supply and primary production in Clear Lake, Eastern Ontario. J. Fish. Res. Board Can. 27: 2009–2036.

STRICKLAND, J. D. H., AND T. R. PARSONS. 1968. A practical handbook of sea water analysis. Bull. Fish. Res. Board Can. 167: 311 p.

UNESCO. 1966. Determination of photosynthetic pigments in seawater. Monogr. Oceanogr. Methodol. 1.

VOLLENWEIDER, R. A. 1969. The possibilities and limits of elementary models concerning the budget of substances in lakes. Arch. Hydrobiol. Board 66: 1–36.

Concentrations of Nutrients and Chlorophyll on a Cross-Channel Transect in Juan de Fuca Strait, British Columbia

A. G. LEWIS

Institute of Oceanography, University of British Columbia, Vancouver, B.C. V6T 1W5

LEWIS, A. G. 1978. Concentrations of nutrients and chlorophyll on a cross-channel transect in Juan de Fuca Strait, British Columbia. J. Fish. Res. Board Can. 35: 305–314.

Nutrient and chlorophyll values were measured hourly at one of four stations on a cross-channel transect, over a 25-h period during each of 5 mo. Nitrate values increased with depth, chlorophyll decreased, and phosphate remained essentially unchanged during most months. Chlorophyll and phosphate values did not show consistent cross-channel trends, while nitrate levels were frequently higher on the southern side of the Strait. The cross-channel nitrate pattern can be at least partially explained in terms of geostrophic flow; greater amounts of nitrate-rich oceanic water enter at depth on the southern side of the Strait, while nitrate poor inshore water exists near the surface on the northern side.

Key words: nutrients, chlorophyll, Juan de Fuca Strait

LEWIS, A. G. 1978. Concentrations of nutrients and chlorophyll on a cross-channel transect in Juan de Fuca Strait, British Columbia. J. Fish. Res. Board Can. 35: 305–314.

Nous avons mesuré les concentrations d'éléments nutritifs et de chlorophylle à toutes les heures à l'une de quatre stations le long d'une section transversale du chenal, sur une période de 25 h par mois pendant 5 mo. Les nitrates augmentent avec la profondeur, la chlorophylle diminue et les phosphates demeurent essentiellement les mêmes durant la plupart des mois. Les niveaux de chlorophylle et de phosphates ne montrent pas de tendance uniforme d'une extrémité à l'autre du chenal, alors que ceux des nitrates sont souvent plus élevés sur le côté méridional du détroit. La distribution des nitrates d'un côté à l'autre du chenal peut s'expliquer en partie du moins en termes d'écoulement géostrophique : un plus grand volume d'eau océanique, riche en nitrates, pénètre en profondeur sur le côté méridional du détroit, alors que l'eau côtière, pauvre en nitrates, se trouve près de la surface sur le côté septentrional.

Received May 26, 1976
Accepted December 8, 1977

Reçu le 26 mai 1976
Accepté le 8 décembre 1977

JUAN DE FUCA Strait is a complex, deep, positive estuary (Herlinveaux and Tully 1961) that forms the major connection between the Strait of Georgia (and Puget Sound) and the North Pacific. Inflowing deep water has oceanic characteristics; outflowing shallow water has Strait of Georgia properties. Mixing within the Strait causes some change in the characteristics, although the transport of oceanic water landward is shown by the salinity structure of the water in the Strait of Georgia (Herlinveaux and Tully 1961; Waldichuk 1957). Little is known about the nutrient levels of water passing through Juan de Fuca Strait and their effect on levels in the Strait of Georgia. Seasonal upwelling near the mouth of Juan de Fuca Strait (Herlinveaux and Tully 1961) could, for example, provide nitrate-rich water that would be carried into the Strait of Georgia.

One of the purposes of the present study was to measure nutrient and chlorophyll levels in Juan de Fuca Strait. The second was to examine cross-channel changes and to relate them to transport of nutrients and chlorophyll through the Strait. (Since flow in the Strait is of a geostrophic nature (Herlinveaux and Tully 1961), changes could occur across the channel.)

Printed in Canada (J4370)
Imprimé au Canada (J4370)

Infrequent measurements of nutrients and chlorophyll can provide an indication of seasonal changes but not short-term fluctuations. Water transport through Juan de Fuca Strait is due to tidal forces as well as river runoff. Geostrophic flow and tidal forces could produce a tidally changing north–south slope of salinity and nutrient isopleths. To estimate tidal effect it was essential to obtain cross-channel values during complete tidal cycles. An understanding of nutrient transport through the Strait is also dependent upon knowledge of tidally produced changes of nutrients.

Materials and Methods

During March–December 1973 a study of the current pattern in Juan de Fuca Strait was undertaken by the Department of the Environment (Canada), Department of Oceanography (University of Washington), and the Institute of Oceanography (University of British Columbia). The University of British Columbia's part of the study (June–December) included monthly monitoring of hydrographic conditions at four stations on a cross-channel transect (Table 1, Fig. 1, 2), over a complete tidal cycle (25-h period). In conjunction with this, nutrients and chlorophyll were measured at selected depths at each station. These values were used to determine levels and cross-channel changes of nutrients and chlorophyll.

TABLE 1. Station locations, cruise numbers, dates, and time (hour 1 Greenwich Mean Time, GMT) of the 25-h cruise program. Equipment failure prevented completion of the October cruise.

Stn.	Lat.	Long.
1	48°21.8′N	124°3.7′W
2	48°19.4′N	124°5.4′W
3	48°17.8′N	124°6.3′W
4	48°15.5′N	124°7.5′W

IOUBC cruise no.	Dates (1973)	GMT
73-22	June 12	1.0
73-27	July 16–17	17.3
73-31	Aug. 13–14	17.4
73-36	Sept. 10–11	17.0
73-44	Nov. 5–7	23.3
73-48	Dec. 4–5	0.6

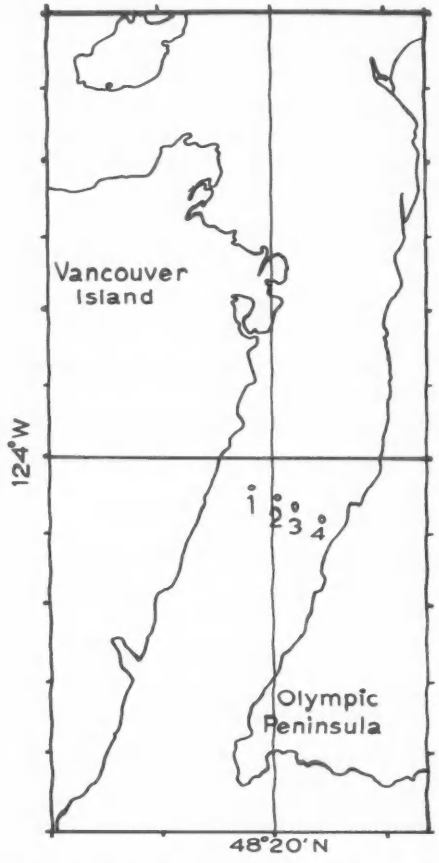

FIG. 1. Juan de Fuca Strait, situated between Vancouver Island on the north and the Olympic Peninsula on the south. The four stations on the transect are shown midway in the Strait.

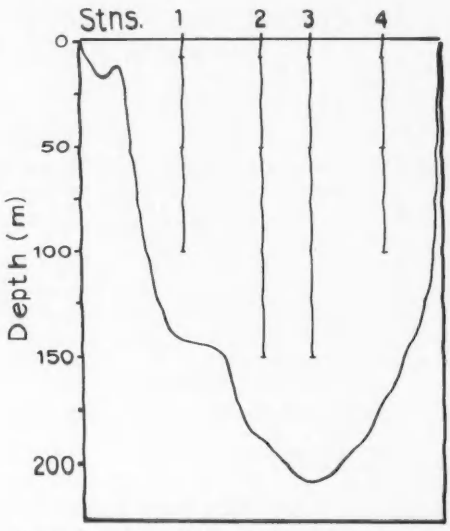

FIG. 2. Section through Juan de Fuca Strait at the position of the transect showing the stations, the depth of sampling at each station, and the depth of the nutrient samples (horizontal marks at 10, 50, and 100 or 150 m).

One station on the cross-channel transect was occupied each hour. Station 3 was occupied at hour 1, station 4 at hour 2, followed by stations 3, 2, 1 . . ., to hour 25 (station 3). The routine remained essentially the same at all stations except for hours 1 and 25 (station 3). The normal station routine included an STD cast (salinity–temperature–depth recorder, Bissett-Berman 9060 or InterOcean 550) to 100 m (stations 1 and 4) or 150 m (stations 2 and 3). Water was collected for nutrient and chlorophyll analysis with either N.I.O. bottles (National Institute of Oceanography, England) or 5-L Niskin bottles, at 10, 50, and 100 m (stations 1 and 4) or 150 m (stations 2 and 3). (Data from June, cruise 22, are not presented because the 50-m sample was not collected.) In addition to the normal program at hours 1 and 25 (station 3), an additional bottle cast (1, 10, 30, 50, 75, 100, 150 m) was made for nutrients, chlorophyll, and hydrographic data.

Water for nutrient analysis was transferred (unfiltered) immediately after collection to polyethylene bottles (200 mL in 250-mL bottle for nitrate, 110 mL in 125-mL bottle for phosphate). The bottles were placed in a freezer as soon as they were filled. For chlorophyll, 1 L of water was transferred to a sample-rinsed polyethylene bottle for subsequent treatment as described in Strickland and Parsons (1972). Concentrations of chlorophyll *a* and reactive nitrate and phosphorous were determined as described in Strickland and Parsons (1972). To reduce the effect of not filtering, turbidity blanks were measured with the reactive phosphorous. The conditions of analysis of reactive phosphorous are such (0.23 N H_2SO_4) that some organophosphate esters will be hydrolyzed and added to the total level. Owing to the spectrophotometer used (Coleman 124), measurements of reactive phosphorous were made at 810 nm, not 885 as recommended. At this wavelength, the factor "F" (Strickland and Parsons 1972, p. 52) was found at be 7.3.

TABLE 2. Correlation coefficients for values obtained at hours 1 and 25 (station 3) from hydrographic and STD casts. (N = 70 for each parameter)

	Phosphate	Nitrate	Chlorophyll *a*	Temp	Salinity	Oxygen	Sigma-t	Temp (STD)
Nitrate	0.35							
Chlorophyll *a*	−0.11	−0.36						
Temp	−0.28	−0.70	0.62					
Salinity	0.38	0.90	−0.29	−0.78				
Oxygen	−0.38	−0.84	0.43	0.77	−0.94			
Sigma-t	0.38	0.90	−0.35	−0.84	0.99	−0.94		
Temp[a] (STD)	−0.21	−0.72	0.68	0.99	−0.76	0.82	−0.82	
Salinity[a] (STD)	0.35	0.89	−0.25	−0.77	0.98	−0.94	0.98	−0.78

[a]Values were taken from the STD record at the depth of each bottle on the hydrographic cast.

TABLE 3. Regressions of nitrate (Y) against salinity (X) for July, August, September, November, and December data.

Month	Cruise no.	Regression	N	Mean square deviation from regression
July	27	$Y = -144.9+5.36X$	76	3.2
Aug.	31	$Y = -93.3+3.70X$	78	3.9
Sept.	36	$Y = -131.4+4.86X$	83	3.6
Nov.	44	$Y = -14.1+1.31X$	78	0.4
Dec.	48	$Y = -158.3+5.72X$	72	8.2

Precision of the techniques was determined by analysis of subsamples from the same Niskin bottle. The mean of six reactive phosphate measurements was 2.42 μg-atoms (at)/L with SD = 0.02. The mean of five reactive nitrate samples was 33.62 μg-at/L ± 0.47 (1 SD). The mean of five chlorophyll *a* samples was 1.72 mg/m³ ± 0.03.

With the hourly sampling schedule necessary to obtain adequate hydrographic coverage of the transect, only three depths could be sampled for nutrients at each station. Data for these three depths are plotted for each cruise in Fig. 3–7. Changes in values with time suggested changes in the water column that could better be discussed with profiles. To determine if estimates of unsampled depths could be made, nutrient and chlorophyll data from the hours 1 and 25

TABLE 4. Average nitrate, chlorophyll, and phosphate values for cruises 27, 31, 36, 44, and 48. (NO_3 = microgram-atoms per litre, Chl = milligrams per cubic metre, PO_4 = microgram-atoms per litre.)

	Stn. 1			Stn. 2			Stn. 3			Stn. 4		
Item	10 m	50 m	100 m	10 m	50 m	100 m	10 m	50 m	100 m	10 m	50 m	100 m
					Cruise 27 (July)							
NO_3	21.45	23.56	32.41	20.93	26.80	33.08	22.05	28.44	33.08	24.02	30.03	31.56
Chl	5.13	1.46	1.12	5.16	1.11	0.72	3.63	1.09	0.74	3.01	0.94	0.86
PO_4	6.41	2.06	2.74	3.36	2.07	2.54	2.35	2.00	2.39	2.05	3.38	2.24
					Cruise 31 (Aug.)							
NO_3	23.01	26.24	32.57	23.05	26.41	33.33	22.35	27.50	32.35	23.11	25.74	30.55
Chl	2.26	0.90	0.82	2.25	0.78	0.51	2.26	0.66	0.49	2.18	0.62	0.56
PO_4	1.73	1.92	2.44	1.67	1.81	2.09	1.66	2.08	2.22	1.74	1.85	1.77
					Cruise 36 (Sept.)							
NO_3	20.51	27.37	32.77	21.91	28.08	32.80	20.45	29.67	32.93	22.21	29.16	30.10
Chl	5.49	1.08	0.83	5.19	0.90	0.62	8.12	0.85	0.61	6.39	0.85	0.68
PO_4	1.91	2.26	2.69	1.94	2.33	2.69	1.79	2.42	2.59	1.91	2.33	2.40
					Cruise 44 (Nov.)							
NO_3	27.08	26.78	29.93	27.43	27.49	30.44	27.67	27.97	30.01	26.80	28.53	28.24
Chl	0.93	0.90	0.62	0.89	0.82	0.54	0.93	0.69	0.53	0.96	0.60	0.53
PO_4	2.31	2.26	2.48	2.31	2.32	2.49	2.30	2.32	2.43	2.18	2.32	2.31
					Cruise 48 (Dec.)							
NO_3	10.33	21.02	25.24	13.06	22.07	26.95	13.20	20.93	26.77	9.15	12.95	25.48
Chl	1.05	0.75	0.69	1.18	0.69	0.71	1.30	0.73	0.60	1.10	0.87	0.54
PO_4	1.12	1.89	2.15	1.29	1.93	2.34	1.29	1.87	2.29	1.03	1.33	2.18

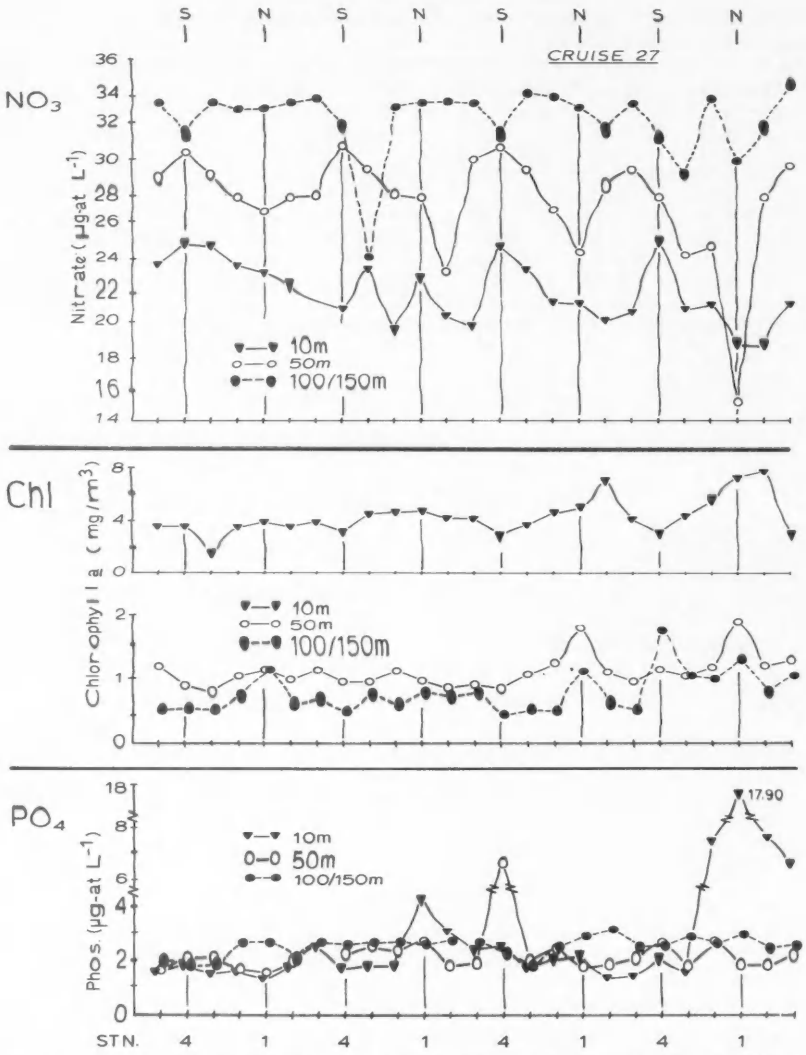

FIG. 3. Measured nitrate, chlorophyll, and phosphate values for cruise 27 (July 1973). Vertical lines mark ends of four-station cross-channel transect. S = southern end of transect (station 4), N = northern end (station 1).

bottle casts were compared with hydrographic data from the bottle cast and the STD cast. These comparisons also permit some expression of distribution of nonconservative properties (nutrients and chlorophyll) in terms of conservative properties (salinity and temperature). Results (Table 2) show that the salinity-nitrate, sigma-t-nitrate, and STD salinity-nitrate correlations approached levels that would allow consideration. Because of the influence of salinity on density in Juan de Fuca Strait, it was used to estimate nitrate values from unsampled depths at the transect stations, for the profiles.

Estimates of nitrate values for unsampled depths (1, 30, 75 m at hours 2–24) were obtained from the regression of measured nitrates against salinities for each cruise (Table 3). Measured as well as estimated values were combined as a matrix through which contours were drawn to depict changes of nitrate with depth and time. Contours were drawn with the "UBC CNTOUR" program. Two of the profiles (Fig. 8, 9) are presented to show trends in nitrate distribution. Because of the influence of tide on movement of water in Juan de Fuca Strait, tidal data were plotted for the same time periods to allow comparison with nitrate changes. Tidal

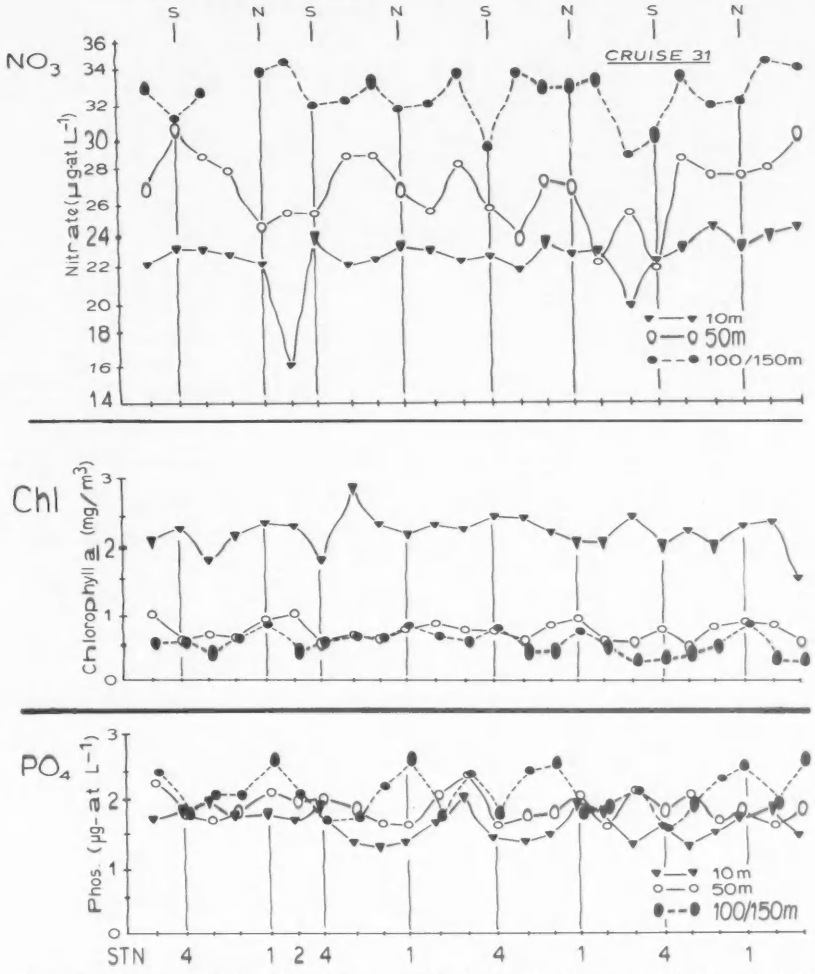

FIG. 4. Measured nitrate, chlorophyll, and phosphate values for cruise 31 (August 1973). Vertical lines mark ends of four-station cross-channel transect. S = southern end of transect (station 4), N = northern end (station 1).

levels used were those from Sooke, British Columbia, the nearest point of continuous measurement.

Original data on salinity and temperature values are in Crean and Lewis (1976). Original data on nitrates, phosphates, and chlorophyll *a* are available in Lewis (1976).

Results

Average phosphate values did not indicate any consistent trends (Table 4, Fig. 3–7). Values tended to be lower near the surface, although in July they were higher at two of the four stations on the transect. Averages were also higher in July (cruise 27), although this was due to several exceptionally high values. These values occurred between hours 22 and 25 (Fig. 3), at a change in tide (Fig. 8). The hour 25 hydro cast value was also high near the surface, reaching 15.60 μg-at/L at 1 m (Lewis 1976).

As expected, average chlorophyll values were higher at 10-m depth than at 50 m and 100/150 m (Table 4, Fig. 3–7). Values at 10 m ranged from <1 mg/m^3 to over 8, being highest in July and September and lowest in November (Table 4). Only in July was there indication of a cross-channel trend (Fig. 3). This occurred during the major ebb tide (Fig. 8), with higher values found towards the northern side of the Strait.

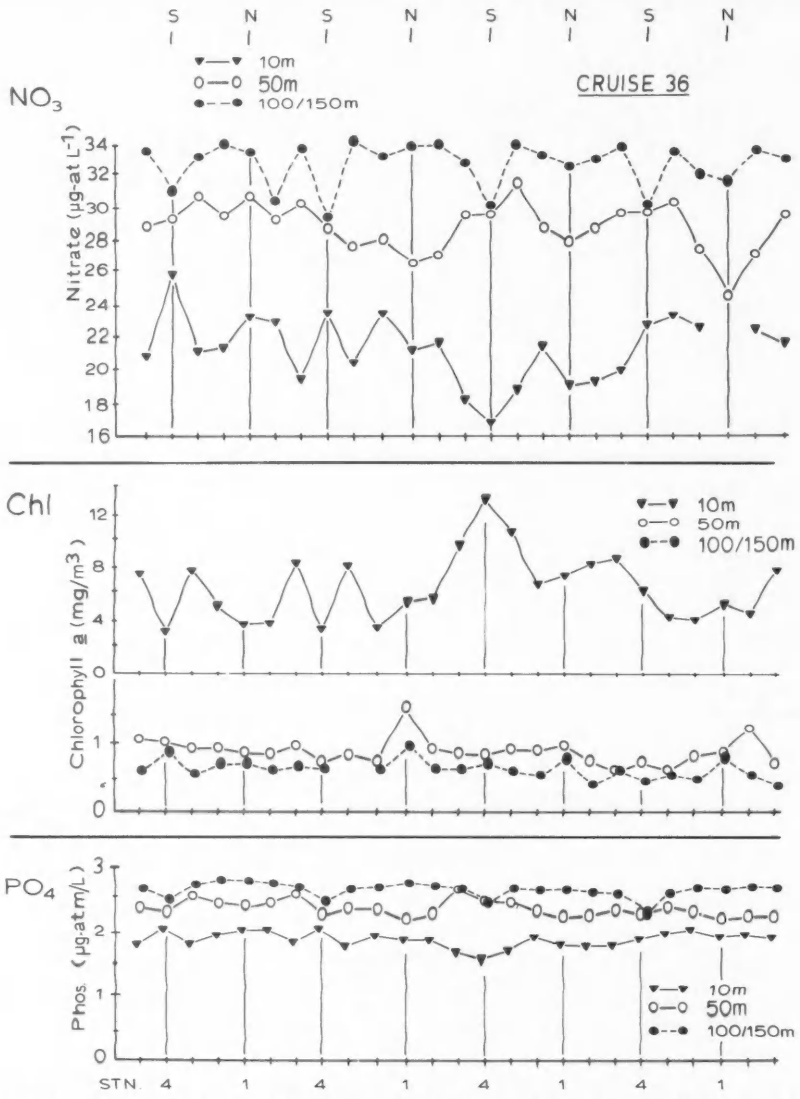

FIG. 5. Measured nitrate, chlorophyll, and phosphate values for cruise 36 (September 1973). Vertical lines mark ends of four-station cross-channel transect. S = southern end of transect (station 4), N = northern end (station 1).

Reactive-nitrate values increased with depth, 10-m averages ranging from ca. 9–27 µg-at/L, and 100/150-m averages from ca. 25–33 µg-at/L (Table 4, Fig. 3–7). Lowest averages occurred in December with a drop in the 10-m values of more than 50% from November. Although station averages do not show obvious cross-channel trends, they are apparent in the individual values in July and November (Fig. 3, 6). Nitrate values increased toward the southern side of the Strait during these two months. Cross-channel trends were best shown by the 50-m values and less so by the 10 m. There were no obvious trends in the 100/150-m values. In several months there was a gradual decline in nitrate during periods when tidal exchange was small. This is shown in the December nitrate profile (Fig. 9), by the deepening of the 24 µg-at/L isopleth during hours 2–10.

An abrupt drop occurred in the 50-m values on the

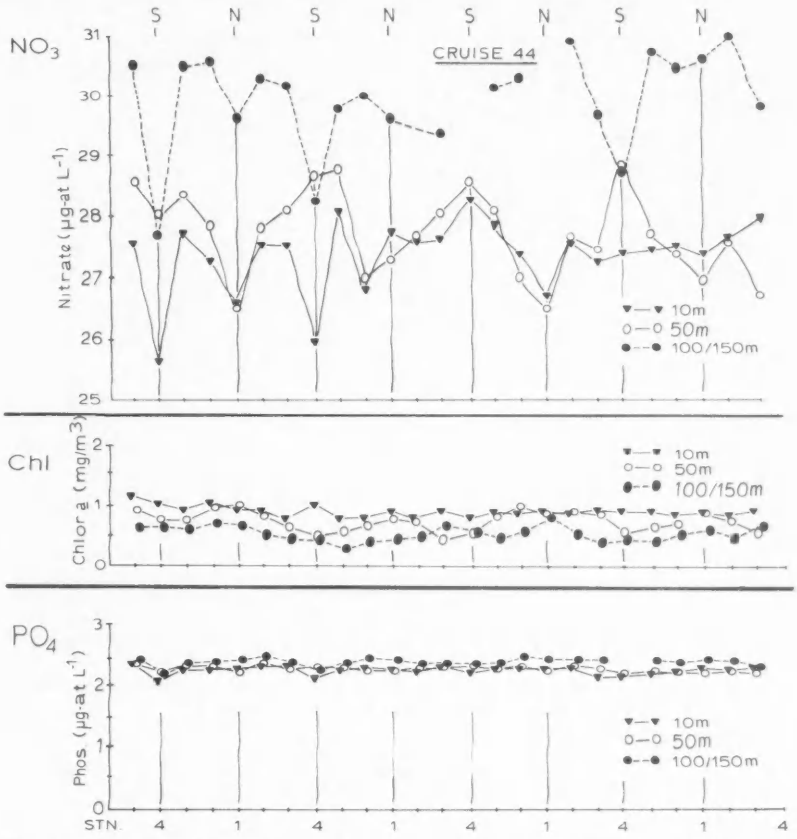

FIG. 6. Measured nitrate, chlorophyll, and phosphate values for cruise 44 (November 1973). Vertical lines mark ends of four-station cross-channel transect. S = southern end of transect (station 4), N = northern end (station 1).

southern side of the Strait in December (Fig. 7). The nitrate profile (Fig. 9) shows a deepening of the 12, 16, and 20 µg-at/L isopleths at hour 2, during a time of little tidal exchange. Between hours 2 and 8 all three isopleths penetrated deeper into the water column. By hour 14, after the turn of the tide, the three isopleths returned to depths similar to those of hour 2, with the 16 and 20 µg-at/L isopleths spreading out. A similar situation was found in July (Fig. 8), with the 21–27 µg-at/L isopleths, between hours 11 and 23. During July, however, the situation occurred during the main ebb tide of the day.

Discussion

The extremely high phosphate values that occurred over a 4-h period in July were in near-surface water and were found shortly after a tidal change, following a long ebb tide. Although contamination must be considered, their occurrence at three stations, during the same time period, suggests the possibility of some high phosphate source or concentrating mechanism. (Since the samples were not filtered, they may represent a source of particulate phosphorous.) The association with a change in tide suggests that the mechanism may have operated along the tide line.

Of the three parameters, only chlorophyll and nitrate changed with depth. Near-surface utilization of nitrate-nitrogen by phytoplankton and dilution by nutrient poor runoff would affect nitrate distribution in the upper part of the water column. Utilization would increase during the summer due to increased phytoplankton levels. This would cause a greater decrease of nitrate-nitrogen above the pycnocline. Mixing of the water column during late fall and winter would bring nitrate-rich deeper water to the surface. The combination of decreased phytoplankton levels and increased mixing at this time of the year would result in greater homogeneity of nitrate in the water column and higher near-surface values. This was evidenced by the 10-m nitrate averages for November (Table 4). A drop oc-

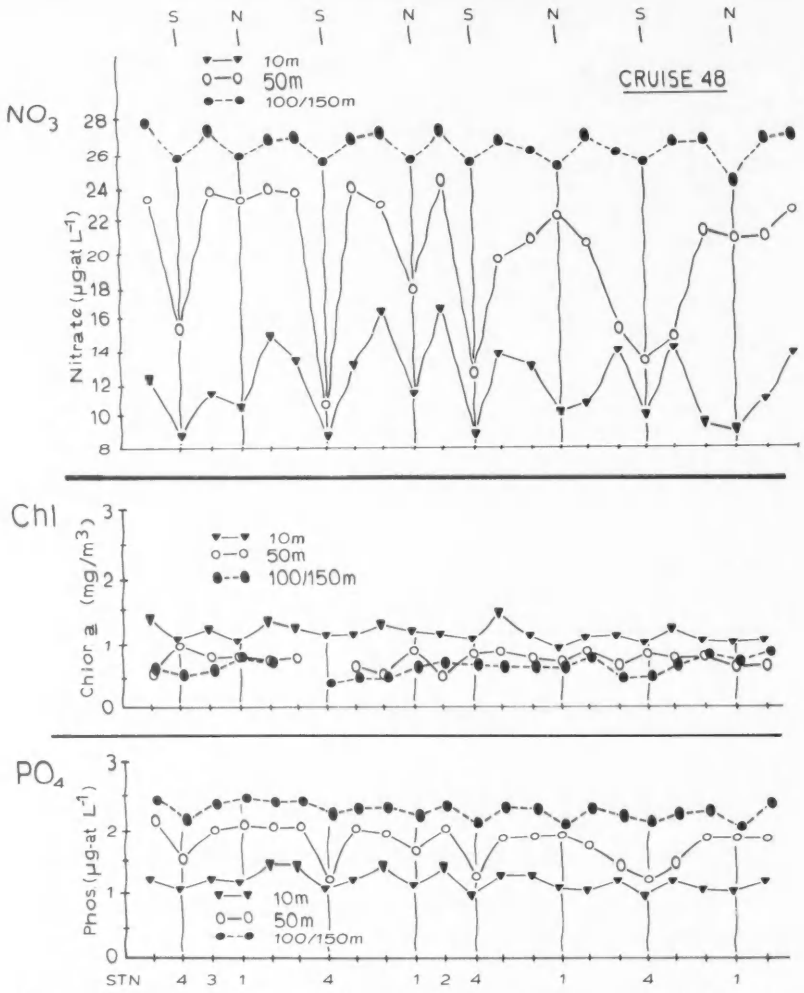

FIG. 7. Measured nitrate, chlorophyll, and phosphate values for cruise 48 (December 1973). *Vertical lines mark ends of four-station cross-channel transect. S = southern end of* transect (station 4), N = northern end (station 1).

curred in the 10-m averages between November and December (Table 4). This may be due to continued mixing with low-nitrate runoff water at the surface and subsequent loss through flow out of Juan de Fuca Strait. Relatively low levels of nitrate throughout the water column in December, however, suggest a change in the nature of the entire water column between the two months. Part of this may be due to a reduction in the amount of nitrate-rich deep oceanic water in the Strait at this time of the year (e.g. Herlinveaux and Tully 1961). Part may also be due to the presence of Davidson Current near-surface water in the winter, bringing nitrate-poor Columbia River runoff water from the south (Conomos et al. 1972; Barnes et al. 1972).

From the nitrate profiles (Fig. 8, 9) there appear to be two parts to the water column. The upper part, above about 80 m, is where nitrate values decrease rapidly with depth. Below this, the values increase more gradually. Nitrate values are highest in deep water, although the isopleths frequently vary in an irregular fashion. Deep water includes oceanic water which enters the Strait along the bottom (Herlinveaux and Tully 1961). Because of geostrophic flow, more oceanic water is found along the southern side of the Strait than along the northern. This is evidenced by the slope of the salinity isopleths (Herlinveaux and Tully 1961) and is also shown by the nitrate values during July and November (Fig. 3, 6, 8). Nitrate values in the upper part of the water column during these months are higher on the southern side than on the northern

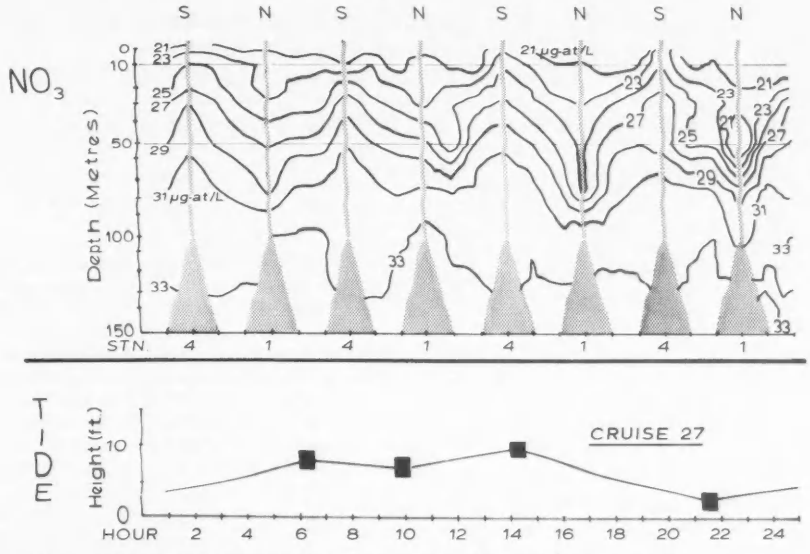

FIG. 8. Nitrate profiles and tidal levels for cruise 27 (July). Nitrate isopleths are given in microgram-atoms per litre. Vertical bars mark ends of four-station cross-channel transect. S = southern end of transect (station 4), N = northern end (station 1). Depths of deepest measured sample at each station are connected and form bottom of profile. Lower figure shows the tidal heights at the nearest point of continuous measurement (Sooke). Maximum and minimum tidal heights are joined by a straight line for comparison with nitrate profiles.

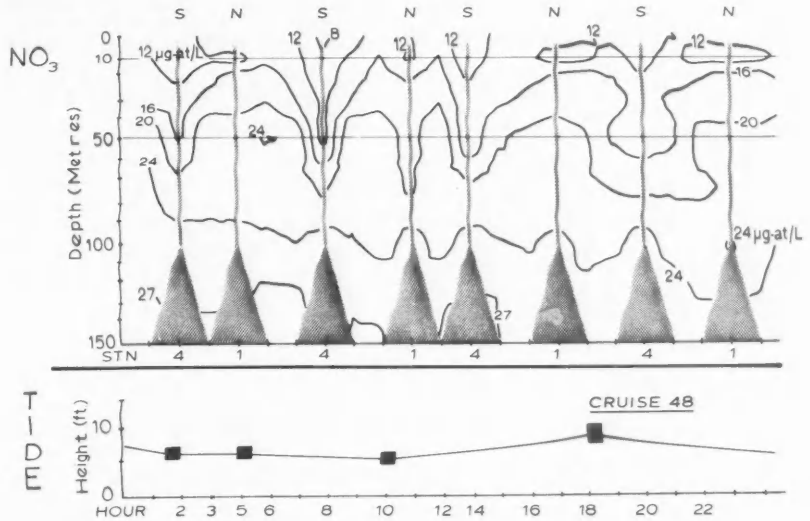

FIG. 9. Nitrate profiles and tidal levels for cruise 48 (December). Nitrate isopleths are given in microgram-atoms per litre. Vertical bars mark ends of four-station cross-channel transect. S = southern end of transect (station 4), N = northern end (station 1). Depths of deepest measured sample at each station are connected and form bottom of profile. Lower figure shows the tidal heights at the nearest point of continuous measurement (Sooke). Maximum and minimum tidal heights are joined by a straight line for comparison with nitrate profiles.

or Vancouver Island side of the Strait.

Not only do the lowest near-surface nitrate values frequently occur on the northern side of the Strait, but so do the highest deep values (e.g. Fig. 8, hours 6-14). Greatest outflow of low-salinity near-surface water also occurs along this side (Herlinveaux 1954). This water

comes from the Strait of Georgia and Puget Sound and is low in nitrates (e.g. Parsons et al. 1970) when compared with Juan de Fuca deep water. The effect of this low-nitrate outflow water would be to produce lower near-surface nitrate values on the northern side. Outflowing near-surface water could also cause entrainment of nitrate-rich subsurface water which would give the extremes in values seen on the northern side of the Strait.

When tidal exchange is small over an extended period of a tidal cycle, there may be a gradual reduction of nitrate in deep water. This is shown by the deepening of the 24-μg-at isopleth in December, during hours 2–10 (Fig. 9). Penetration of low-nitrate shallow water into deeper water may also occur, as is shown by the abrupt drop in 50-m values on the southern side of the Strait in December (Fig. 7). This is at a time when deep water values are decreasing and may be a result of down-mixing of near-surface low-nitrate water.

Although nitrogen transport estimates are premature with the present data, rough estimation can be of value in determining the importance of Juan de Fuca Strait in supplying the Strait of Georgia and Puget Sound with nitrate-nitrogen. Herlinveaux (1954) and Herlinveaux and Tully (1961) provide an estimate of net transport above and below the depth of no-net motion in Juan de Fuca Strait. (Note that Herlinveaux (1954) gives net transport in cubic feet over a tidal cycle, but Herlinveaux and Tully incorrectly give the same value as net transport in cubic feet per second (R. H. Herlinveaux, Institute of Ocean Sciences, 9860 West Saanich Road, Sidney, B.C., personal communication.)) Net seaward transport, above the depth of no-net motion, is 1.984×10^{10} m^3/day, while net inflow, below the depth of no-net motion, is 1.512×10^{10} m^3/day. To relate this to nitrate-nitrogen transport, it was assumed that the depth of no-net motion occurred between 75 and 100 m at station 1 (Fig. 2), between 50 and 75 m at station 2, and between 30 and 50 m at stations 3 and 4. Average nitrate values above and below the depth of no-net motion were calculated from the matrix values for the nitrate profiles for each of the 5 mo. The average of all of these was assumed to be representative for the entire year. Net loss of nitrate was then calculated for the seaward-moving water above the depth of no-net motion, as was net gain of nitrate below the depth. (Input of nitrate from rivers is essentially nil, so that all the nitrate was considered to be accounted for by the seawater values.) The difference between the nitrate-nitrogen input and loss from Juan de Fuca Strait, over a yearlong period, amounts to a net gain of approximately 1.07×10^4 t of nitrogen. This excess is at least partially retained through biological activity in the Strait of Georgia and Puget Sound.

Acknowledgments

Many individuals were involved in the study. These include the officers and crew of the C.S.S. *Vector*, technicians from the Department of the Environment (E. Marles and J. Lanteigne) and from the Institute of Oceanography, UBC (A. Ramnarine, P. Erickson, M. Storm, T. Felton, F. Whitney). Dr M. Miyake was one of the instigators of the study and provided grant funds (NRC A-4295) for one of the technicians. Funds for other UBC technicians, materials, and supplies came from grants to the Institute of Oceanography, UBC, and to A. G. Lewis (NRC A-2067). Discussions with Dr T. Parsons and Dr P. Crean were instrumental in the preparation of the manuscript.

BARNES, C. A., A. C. DUXBURY, AND B. A. MORSE. 1972. Circulation and selected properties of the Columbia River effluent at sea. *In* A. T. Pruter and D. L. Alverson [ed.] The Columbia River estuary and adjacent ocean waters. University of Washington Press, Seattle, Wash.

CONOMOS, T. J., M. G. GROSS, C. A. BARNES, AND F. A. RICHARDS. 1972. River–ocean nutrient relations in summer. *In* A. T. Pruter and D. L. Alverson [ed.] The Columbia River estuary and adjacent ocean waters. University of Washington Press, Seattle, Wash.

CREAN, P., AND A. G. LEWIS. 1976. Monthly sections, Strait of Juan de Fuca, June–December 1973. Inst. Oceanogr., Univ. British Columbia, Data Rep. 39: 218 p. (provisional)

HERLINVEAUX, R. H. 1954. Tidal currents in Juan de Fuca Strait. J. Fish. Res. Board Can. 11: 799–815.

HERLINVEAUX, R. H., AND J. P. TULLY. 1961. Some oceanographic features of Juan de Fuca Strait. J. Fish. Res. Board Can. 18: 1027–1071.

LEWIS, A. G. 1976. Monthly nutrient and chlorophyll values for Juan de Fuca Strait, June–December 1973. Inst. Oceanogr., Univ. British Columbia, Data Rep. 40: 20 p.

PARSONS, T. R., R. J. LEBRASSEUR, AND W. E. BARRACLOUGH. 1970. Levels of production in the pelagic environment of the Strait of Georgia, British Columbia: A review. J. Fish. Res. Board Can. 27: 1251–1264.

STRICKLAND, J. D. H., AND T. R. PARSONS. 1972. A practical handbook of seawater analysis. Bull. Fish. Res. Board Can. 167: 310 p.

WALDICHUK, M. 1957. Physical oceanography of the Strait of Georgia, B.C. J. Fish. Res. Board Can. 14: 321–486.

Concentrations and Kinetics of Phosphorus Fractions in Water from Streams Entering Lake Memphremagog[1]

ROBERT HENRY PETERS

Department of Biology, McGill University, Montreal, Que. H3A 1B1

PETERS, R. H. 1978. Concentrations and kinetics of phosphorus fractions in water from streams entering Lake Memphremagog. J. Fish. Res. Board Can. 35: 315–328.

This study examines the possibility that the proportions of different P fractions may vary among rivers, and hence, that the P supplied to lakes may differ in its availability for algae regardless of any similarities in the total P concentration of river waters. Surface water from eight streams and groundwater was collected at roughly monthly intervals from June 1975 to September 1976 and analyzed to determine the concentrations of P fractions and the interrelations between these forms and orthophosphate. Despite differences in total P concentration, (18–64 μg/L) the proportions of P in different fractions were relatively constant seasonally and geographically. Soluble P formed about one third and PO_4 <10% of the total P. These values were not greatly affected by urban drainage but both were increased in small headwater streams during periods of low water. Soluble P was divided into two roughly equal fractions by gel filtration: a large molecular weight fraction (>5000 mol wt) which eluted at void volume and a small molecular weight fraction (<400 mol wt) which eluted with ^{32}P-PO_4. This latter fraction also included some small organic phosphates. Soluble reactive phosphate consistently overestimated PO_4. The exchange of P between PO_4 and suspended material was slow in winter and more rapid in summer, although only rivers draining lakes, embayments, or bogs reached the very rapid values reported from lakes. As in lakes, soluble organic P entered into the short-term P dynamics of streams as indicated by the labeling of large molecular weight P during equilibration of river water with radioactive phosphate. This exchange shows that at least a portion of the soluble organic and particulate P is available to the plankton once the river water enters a lake. The uncertainty as to the size of this portion leads to uncertainty in predicting the impact of P loading on lakes.

Key words: nutrient budget, P loading, orthophosphate, soluble organic P, drainage basins

PETERS, R. H. 1978. Concentrations and kinetics of phosphorus fractions in water from streams entering Lake Memphremagog. J. Fish. Res. Board Can. 35: 315–328.

L'auteur examine la possibilité de variations dans les proportions des différentes fractions de P selon les rivières et de là, de différences dans la disponibilité pour les algues du P parvenant aux lacs malgré toute similitude dans le P total des tributaires. De juin 1975 à septembre 1976, les eaux de surface de huit tributaires et nappes phréatiques furent prélevées et analysées pour en déterminer la concentration des différentes fractions de P ainsi que les relations entre ces formes et l'orthophosphate. Malgré des différences de concentration de P total (18–64 μg/L), les proportions des différentes fraction de P sont relativement constantes, à la fois saisonnièrement et géographiquement. Le P soluble contribue pour environ un tiers, et le PO_4 pour moins de 10% du P total. Ces valeurs sont peu affectées par le drainage urbain mais augmentent toutes deux dans les petits ruisseaux de tête durant les périodes d'étiage. Le P soluble est divisé en deux fractions approximativement égales : une fraction de poids moléculaire élevé (> 5 000), éluable à volume nul, et une fraction de faible poids moléculaire (< 400) d'élution simultanée au ^{32}P-PO_4. Cette dernière fraction contient également certains phosphates organiques. Le phosphore réactif soluble surestime le PO_4 d'une façon uniforme. L'échange de P entre le PO_4 et la matière particulaire est lent en hiver et plus rapide en été; cependant, seuls les émissaires des lacs, les tourbières ou les marais atteignent les valeurs rapides caractéristiques des lacs. Comme dans les lacs, le P organique soluble participe à la dynamique à court terme du P des cours d'eau tel qu'indiqué par le marquage du P de poids moléculaire élevé pendant l'équilibration de l'eau de rivière avec du phosphate radioactif. Cet échange montre qu'au moins une portion du P organique soluble et du P particulaire est disponible au plancton lorsque l'eau des tributaires arrive au lac. Comme on n'est pas sûr de l'importance de cette portion, il est impossible de prédire avec certitude l'impact de l'apport en P dans les lacs.

Received June 2, 1977
Accepted December 13, 1977

Reçu le 2 juin 1977
Accepté le 13 décembre 1977

[1]A contribution to the Memphremagog Project, McGill University.

Printed in Canada (J4866)
Imprimé au Canada (J4866)

DIFFERENCES in the availability of phosphorus (P) in streams may contribute to the observed variations between measured and predicted effects of a given P load to lakes (Dillon and Rigler 1974). Certainly some naturally occurring forms of P, such as apatite (Golterman 1973; Williams et al. 1976) and orthophosphate (Rigler 1964; Schindler et al. 1973), differ greatly in their availability to algae. Nevertheless most investigators have measured only total P, since the classical limnological fractionation into particulate, soluble reactive, and soluble unreactive P (Strickland and Parsons 1968) is arbitrary (Rigler 1964) and controversial (Rigler 1966, 1968; Walton and Lee 1972). For this study, variations in certain phosphorus fractions among streams tributary to Lake Memphremagog, Vermont–Quebec, were studied in the expectation that differences in the concentrations and activities of these fractions would reflect differences in the availability of the streams' P to lake plankton.

The program had three aspects. The first was the identification in stream waters, of several operationally defined P fractions (orthophosphate or PO_4, large molecular weight P or LMWP, and small molecular weight P or SMWP) which were expected to differ in their relative availabilities (Lean 1973a, b). Second, the changes in these fractions, seasonally and geographically, were followed and compared with each other and with more traditional fractions (total P, soluble P, and soluble reactive phosphorus or SRP). Last, the labeling of these fractions in brief experiments with radioactive orthophosphate (^{32}P-PO_4) was examined to indicate the degree of exchange between a highly available form of P (PO_4) and other fractions (particulate P, LMWP, and SMWP) of unknown availability: the more labeled these fractions became, the more readily available they must have been.

Materials and Methods

STUDY SITE

Between June 1975 and September 1976, samples of surface water were collected at approximately monthly intervals from nine sites on six watersheds. Although all streams drained primarily rural areas of woods and pasture underlain by glacial till and sedimentary rock, streams differed considerably in size and development of the watershed (Table 1).

Occasionally groundwater samples were collected from a simple well consisting of 5.1-cm black polyvinyl chloride piping extending into the water table, close to the shore at the Memphremagog Project's field laboratory on MacPherson Bay, Lake Memphremagog.

CHEMICAL ANALYSES

Total P concentrations were determined on duplicate 50-mL samples of unfiltered river water after these were digested with potassium persulphate (Menzel and Corwin 1965). The oxidized P was then analyzed with the ascorbic acid modification of the molybdenum blue reaction (Strickland and Parsons 1968).

TABLE 1. Geographical coordinates of sites examined in this study, their watershed areas (WA, in km²), preliminary estimates (R. Carlson unpublished data) of their percentage contribution to the annual P load of Lake Memphremagog (%), and some salient aspects of their drainage basins.

Site	Lat., Long.	WA	%	Drainage
Fitch Bay rivers				
MacPherson Ck.	45°07′N, 72°15′W	14.6	0.1	Upland forest
Bunker Bk.	45°07′N, 72°11′W	14.0	0.6	Low-lying forest
Fitch Ck.	45°07′N, 72°10′W	62.2	1.4	Lake Lovering forest, pasture
The Narrows	45°08′N, 72°09′W	113	3.3	Fitch Bay
South Bay rivers				
Barton R.	44°52′N, 72°12′W	451	25	Forest, pasture farms
Black R.	44°55′N, 72°11′W	347	13	Forest, pasture farms
South Bay	44°56′N, 72°12′W	798	38	Barton and Black R.
Clyde above outfall	44°56′N, 72°12′W	368	15	Clyde Pond, forest, pasture farms
Clyde below outfall	44°56′N, 72°12′W	368	53	Newport, Clyde above outfall

Within 4 h of collection, 250 mL of whole river water were filtered through a prewashed (Rigler 1964) 47-mm diameter, 0.45-μm Millipore membrane filter. The filtrate was analyzed for total soluble and soluble reactive P by the techniques described above.

RADIOLOGICAL BIOASSAY FOR ORTHOPHOSPHATE

Since soluble reactive P frequently overestimates PO_4, a modification of Rigler's (1966) radiological bioassay was used to determine PO_4 concentration (Peters 1977).

When ^{32}P-PO_4 is added to lake water, it is rapidly incorporated by the plankton (Rigler 1964; Peters 1975a; Peters and MacIntyre 1976). The uptake is slowed by the addition of orthophosphate carrier, ^{31}P-PO_4 (Rigler 1966). This phenomenon was used to erect a set of standard curves by adding known concentrations of carrier plus ^{32}P-PO_4 dissolved in membrane-filtered lake water to an equal volume of whole lake water from the surface of the central basin of Lake Memphremagog. Aliquots (5 mL) of this mixture were then filtered (0.45-μm Millipore membrane) at set intervals (usually 2, 8, 15, 30, 45, 60, 90, and 120 min after mixture) and the fraction of tracer removed by filtration was determined. These data were plotted as a family of seven standard curves, like the two curves in Fig. 1 showing the fractional incorporation at each filtration time against the concentration of added PO_4 in the lake water filtrate. Simultaneous experiments, in which filtered ^{32}P-PO_4-labeled river water was added to an equal volume of whole lake water gave the fraction of tracer incorporated in these "unknowns" at each filtration time. Comparisons between these and the standard curves permit estimates of riverine PO_4 concentration above that of filtered lake water, by interpolation. For example, if 5 mL of a 1:1 mixture of whole lake water and filtered river water plus ^{32}P-PO_4 were filtered 2 h after mixture on August 2, 1976, and 75% of the tracer were retained on the filter, interpolation from Fig. 1 would suggest that the river contained approximately 4.8 μg PO_4-P/L more than lake water. This estimate was increased by addition of a maximum estimate of orthophosphate concentration in dilute lake water determined from the data used for the standard curves according to

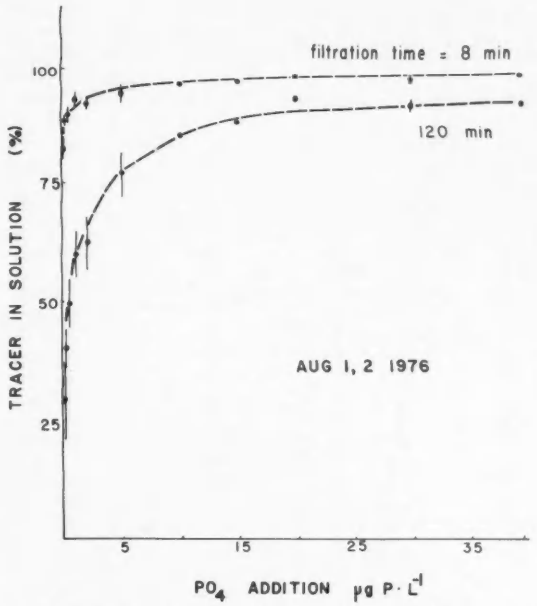

FIG. 1. Standard curves from radiological bioassay of August 1 and 2, 1976. Upper curve gives the percentage of tracer in solution at the first filtration time for a series of PO_4 concentrations. Lower curve represents similar data from the last filtration time. The remainder of this family of standard curves fell between the two. Points give mean values and vertical bars standard deviations at replicated runs. Vertical axis is mislabeled in a similar figure in Peters (1977, fig. 1 and table 1).

Rigler's (1966) radiobiological assay. In all cases, the radioactive tracer was obtained as carrier-free ^{32}P-PO_4 (New England Nuclear Corporation) and radioactivity was determined under gas flow with a Nuclear Chicago Geiger Müller System. Since the assay is most sensitive during periods of rapid PO_4 turnover in the lake water, winter samples were stored frozen until summer.

Gel-Filtration Analysis

Gel-filtration analysis has been used to identify different phosphorus species dissolved in lake water (Minear 1972) and to characterize gross P fractions according to their molecular weight (Peters and Lean 1973; Ferrante 1976; Peters 1977).

In these experiments, a drop of dilute ^{32}P-PO_4 solution, 0.3 g sodium chloride, and 0.03 g sodium azide were dissolved in 50–100 mL of membrane-filtered river water and the solution frozen in polyethylene bottles until analysis was possible. The radioactive tracer served to mark the position of PO_4 in the effluent from the gel column and to control for incorporation of PO_4 by other fractions during handling; the NaN_3 served to reduce bacterial growth in the column; and the NaCl is necessary to obtain significant separation of different fractions. After 1 day to 2 wk the samples were thawed and, usually, 25-mL aliquots were loaded onto two serially joined, 2.5 × 35 cm chromatographic columns filled with G-25 fine Sephadex gel (Pharmacia). During 1975 50-mL aliquots of some samples were loaded onto a 5 × 100 cm column, but this was abandoned in 1976 because of the longer elution time required. The sample was eluted with a solution of 0.3% NaCl and 0.03% NaN_3 in distilled water. Eluant flow was maintained at about 1.5 mL/min with a Buchler Polystaltic pump, and 25-mL fractions of the effluent from the column were collected automatically by an LKB Ultra-Rac fraction collector. Half-millilitre samples of each fraction were dried on planchets and counted for radioactivity to determine the fractions with which PO_4 eluted. The remainder of each fraction was analyzed for total P as described above.

Columns were packed as recommended in the Pharmacia technical bulletins and calibrated before use with ^{32}P-PO_4 and blue dextran (Pharmacia); the latter identified the position of void volume, i.e. the eluant fractions that contain those molecules that are so large (mol wt >5000) that they are excluded by the gel and are therefore the first molecules from the sample to appear in the columns' effluent.

The effects of handling on the Sephadex fractions were examined in water collected at the mouth of South Bay, since this should contain a mixture of P from all four "South Bay" sites (Table 1). Neither freezing nor refiltration affected the amount or distribution of fractions in the columns' effluent. Neither freezing nor the addition of salts led to precipitation of tracer or soluble P. Storage of frozen samples should produce no noticeable absorbtion of phosphorus, since such absorbtion is primarily an effect of bacterial activity (Heron 1962), which would be very low in frozen samples of filtrate, even without the addition of NaN_3.

Orthophosphate Turnover Rate

The rate of uptake of ^{32}P-PO_4 by suspended particles in natural waters is a measure of the interchange between particulate P and orthophosphate.

After collection, 100–500-mL samples of whole river water were placed in plastic beakers and about 1 µCi of carrier-free ^{32}P-PO_4 solution was mixed into each. Thereafter (usually at 2, 4, 8, 15, 30, 60 min and then at increasing intervals up to 2 h in summer and 24 h in winter), 5-mL aliquots of this water were filtered through 25-mm 0.45-µm Millipore membrane filters. The radioactivity of water samples and filters was measured, the percentage of tracer remaining in solution at each filtration time calculated, and the rate constant of orthophosphate uptake, k, estimated with curve-splitting techniques (Riggs 1970; Lean and Rigler 1974), assuming a two-compartment exchange system (Rigler 1973). For brevity, this constant, k, will be referred to either as the "rate constant" or the orthophosphate "turnover rate" (Peters 1975a; Peters and MacIntyre 1976). Its inverse is termed the "turnover time," the time required for uptake of an amount of PO_4 equal to the total dissolved PO_4 pool (Riggs 1970). A sample calculation of k is summarized in Fig. 2. In that case, the assumption of two compartments does not describe the later data points as well as more complex models might. However, this slow portion of the curve was not determined precisely enough to warrant more elegant treatment and any adjustment this might require to estimates of the fast component were minor.

Orthophosphate Transformations

Departures from the two-compartment model suggest the involvement of dissolved P other than orthophosphate in

the short-term dynamics of P exchange (Rigler 1973; Lean and Rigler 1974). This has been confirmed, in lake water, by anomalous uptake curves of the tracer, which remains in solution after equilibration with the plankton (Chamberlain 1968; Lean 1973b, 1976), and by the labeling of large molecular weight fractions in gel filtration. This involvement suggests that other P species besides orthophosphate may be available to the plankton, albeit at slower rates (Lean 1973b).

From December 1975 to September 1976 the degree to which large molecular weight P became labeled during the ^{32}P-PO_4-uptake experiments was examined. At the end of those experiments, 250-mL subsamples of ^{32}P-labeled river water were filtered through prewashed 47-mm diameter, 0.45-μm Millipore filters. A 50-mL portion of radioactive filtrate was mixed with 0.3% NaCl and 0.03% NaN_3 and stored frozen in polyethylene bottles until gel-filtration analysis. The distribution of ^{32}P and ^{31}P in effluent fractions was then determined as described above.

Results and Discussion

Phosphorus Fractions

Despite considerable differences in total P concentration, the proportional distribution of P among the various fractions was very similar in all waters but those from the two smallest streams. These data are summarized in Tables 2 and 3. Since no consistent seasonal patterns were observed, detailed fluctuations in total P, soluble P, and PO_4 concentrations are presented for only four rather different streams (Fig. 3). Detailed summaries may be had by writing to me.

Total P and soluble P — As expected, high values for total P concentration were found in those rivers (Barton, Black, Clyde) with considerable human disturbance in their watersheds. However, high values were also observed in the almost undisturbed Bunker Brook during the summer of 1975. Heavy rains, particularly two storms associated with hurricanes on the east coast of North America on September 28, 1975 and August 1, 1976, caused pronounced increases in total P in most rivers probably by scouring the stream bed and/or by increasing erosion from the watershed. The boggy drainage of Bunker Brook and either the increased volume or increased sedimentation in embayments like the Narrows (Fig. 3) appeared to damp the effect of this heavy precipitation. Similar variations in seasonal pattern have been observed by other authors (Ahl 1972; Hobbie and Likens 1973; Dillon 1974, 1975; Klausner et al. 1974; Hartland-Rowe and Wright 1975; Rich and Palotti, 1977).

In summer the fraction of the total P that passed a 0.45-μm membrane filter (soluble P in Fig. 3 and Table 2) usually varied less than did total P among sites and sampling dates. On average 30–40% of the total P appeared in the filtrate. In winter a higher but more variable fraction appeared in solution. Similar summer proportions have been described in lakes (Rigler 1964) and rivers (Unger 1969). Bunker Brook followed the same pattern, although the proportion in solution was somewhat higher. MacPherson Brook showed quite different values: in summer soluble P formed about 80% of the total and in winter 70%.

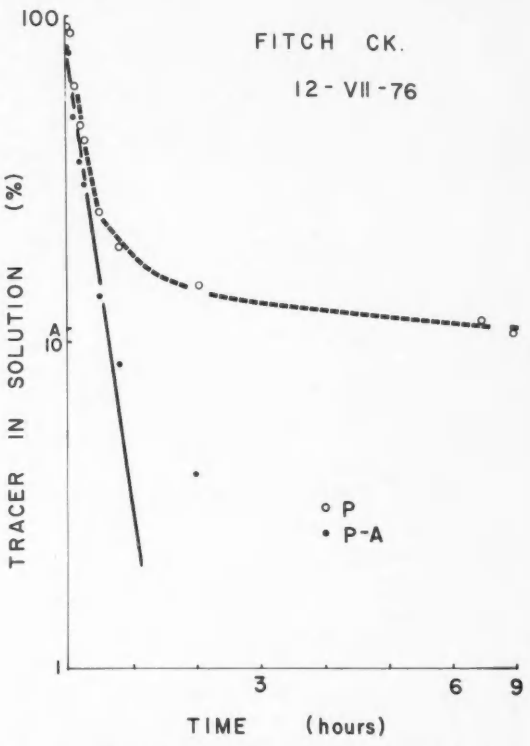

FIG. 2. Calculation of k, the rate constant of orthophosphate uptake. Dashed line gives P, the percentage of tracer in solution at time t, and A is the asymptotic value, the percentage in solution at equilibrium. A plot of P–A yields the solid line; the fractional incorporation of ^{32}P-PO_4 per minute, k, is calculated as 2.303 times the slope of this line.

PO_4 and SRP — Orthophosphate concentrations (Fig. 3, Table 2) were relatively low (6–8% of total P) in all streams except Bunker and MacPherson in 1975, when the average proportions were elevated (13 and 44%, respectively, of total P). Embayments and the Clyde, after Clyde Pond but before the sewage outfall, had somewhat lower fractions of PO_4 (at most, 2–5% of total P). These orthophosphate concentrations were typically lower than those of filtered lake water (mean concentration = 0.8 μg P/L); such concentrations could not be measured with the modified radiobiological assay described above and a maximum estimate of PO_4 concentration in the lake water, as determined by Rigler's (1966) radiological bioassay, was substituted. These values are indicated by circled crosses in Fig. 3. Phosphate concentrations tended to

TABLE 2. Total phosphorus concentration (TP in μg P/L), soluble phosphorus (SP, as % of total), orthophosphate (PO_4, as % of total), soluble reactive phosphorus (SRP, as % of total), and the rate constant of orthophosphate turnover (k, in fraction of PO_4/min) in winter (W, October 1975 through May 1976) and summer (S, June to September in 1975 and 1976). Values are means ± 1 SD.

		TP	SP	PO_4	SRP	k
Black	W	41.9±19.8	36±9.6	2.8±1.5	19±6	0.00076±0.00072
	S	46.6±46.5	33±10	8.9±13	18±11	0.0186±0.0174
Barton	W	43.9±7.4	42±12	2.5±1.0	29±12	0.00159±0.0020
	S	46.6±32.3	36±11	11±5.2	22±8	0.0050±0.0036
Clyde below outfall	W	57.9±32.6	54±15	1.4±1.4	19±18	0.0013±0.0013
	S	63.6±48.6	27±11	8.4±4.7	26±11	0.0100±0.0142
Clyde above outfall	S 1976	31.8±6.6	34±14	2.7±2.3	7.8±5	0.123±0.124
South Bay	W	27.5±14.3	60±26	5.3±0.2	31±21	0.00065±0.00030
	S	29.8±9.8	31±7	5.4±2.9	18±17	0.21±0.30
Narrows	W	20.9±4.9	50±28	2.2±1.0	23±4	0.0040±0.0047
	S	24.3±5.0	28±10	3.5±3.6	21±7	0.23±0.14
Fitch	W	18.2±3.9	52±10	2.0±1.7	15±10	0.0059±0.0061
	S	17.6±12	48±13	8.1±9.8	17±6	0.0151±0.0200
Bunker	S 1975	40.3±18.0	45±8	12.8±7.2	24±22	0.0126
	W	17.7±6.8	71±24	4.9±1.0	22±8	0.0021±0.0017
	S 1976	27.8±8.0	57±9	2.8±2.1	17±22	0.079±0.150
MacPherson	S 1975	6.7±2.1	82±15	44±33	61±23	0.0064
	W	21.4±13.1	69±47	3.5±3.3	21±22	0.00065±0.00046
	S 1976	17.8±13.6	76±38	8.0±8.0	31±22	0.0035±0.0038
Groundwater		5.6±1.6	100	55±51	61±24	—

TABLE 3. Results of gel filtration. The proportion of soluble P (as % of total recovery ± 1 SD) that elutes at void volume (LMWP) and with ^{32}P-PO_4 (SMWP), and in intermediate fractions (i) from rivers and groundwater draining into Lake Memphremagog. All analyses were performed with G-25 fine Sephadex gel and recoveries of ^{32}P-PO_4 and soluble P exceeded 70% of that added.

	LMWP	i	SMWP
Black	41±18	8±8	48±20
Barton	33±20	13±7	34±23
Clyde below outfall	25±16	6±7	64±23
Clyde above outfall	29±14	3±9	59±18
South Bay	43±15	13±10	43±15
Narrows	48±22	9±15	42±24
Fitch	43±18	21±21	38±23
Bunker	41±20	15±13	48±20
MacPherson	53±13	9±8	35±13
Groundwater	35±33	5±3	62±7

decrease in winter in all streams.

Soluble reactive phosphorus (Table 2) usually amounted to 20–30% of the total P. This is somewhat less than the proportion (33–50%) reported in other studies (Ahl 1972; Numann 1967, 1968; Ongley 1976; Barbanti et al. 1974). Nevertheless SRP overestimated orthophosphate concentration (Table 2). As shown in Fig. 4 the amount of overestimation was variable and was apparently unrelated to concentrations of PO_4 or SRP or to land use patterns in the watersheds. (The few points lying well below the 45° line in Fig. 4 probably reflect experimental error in determining PO_4 levels.) In streams, as in lakes (Rigler 1966, 1968) and rain (Peters 1977), SRP is not always a meaningful estimator of PO_4 concentration.

Gel-filtration analyses — Sephadex analysis of soluble P in river water presented several technical difficulties. Frequently recovery of tracer or soluble P was very low (10–70% of that added) and the ^{32}P-PO_4 marker was smeared over many of the effluent fractions. This problem was apparently enhanced by prolonged storage of the water used as eluant, by low PO_4 concentrations in the sample, by the presence of organic material in the sample, and by prolonged use of the columns. Autoclaving the gel and the eluant temporarily removed this effect. These casual observations suggest that low recovery and poor resolution were caused by bacterial contamination of the columns despite the use of distilled, deionized water containing sodium azide as an antibacterial agent. Consequently only samples in which at least 70% of loaded tracer and soluble P was recovered are used in the following discussion. Only 120 runs of the total 189 performed met this criterion; the average recovery in this 63% of all samples was 101% (SD = 20) for ^{32}P and 94% (SD = 20) for soluble P.

Representative results of gel-filtration analyses of river-water filtrates are plotted in Fig. 5. The soluble P in 25 mL of river-water filtrate loaded onto the column was divided unequally among eight 25-mL effluent fractions. Since the soluble P concentrations in many rivers were often low, this further subdivision required that P analyses be performed on some fractions containing <1 μg P/L of lake P. This is at the limits of precision of the molybdenum blue technique. Further uncertainty was introduced because of the

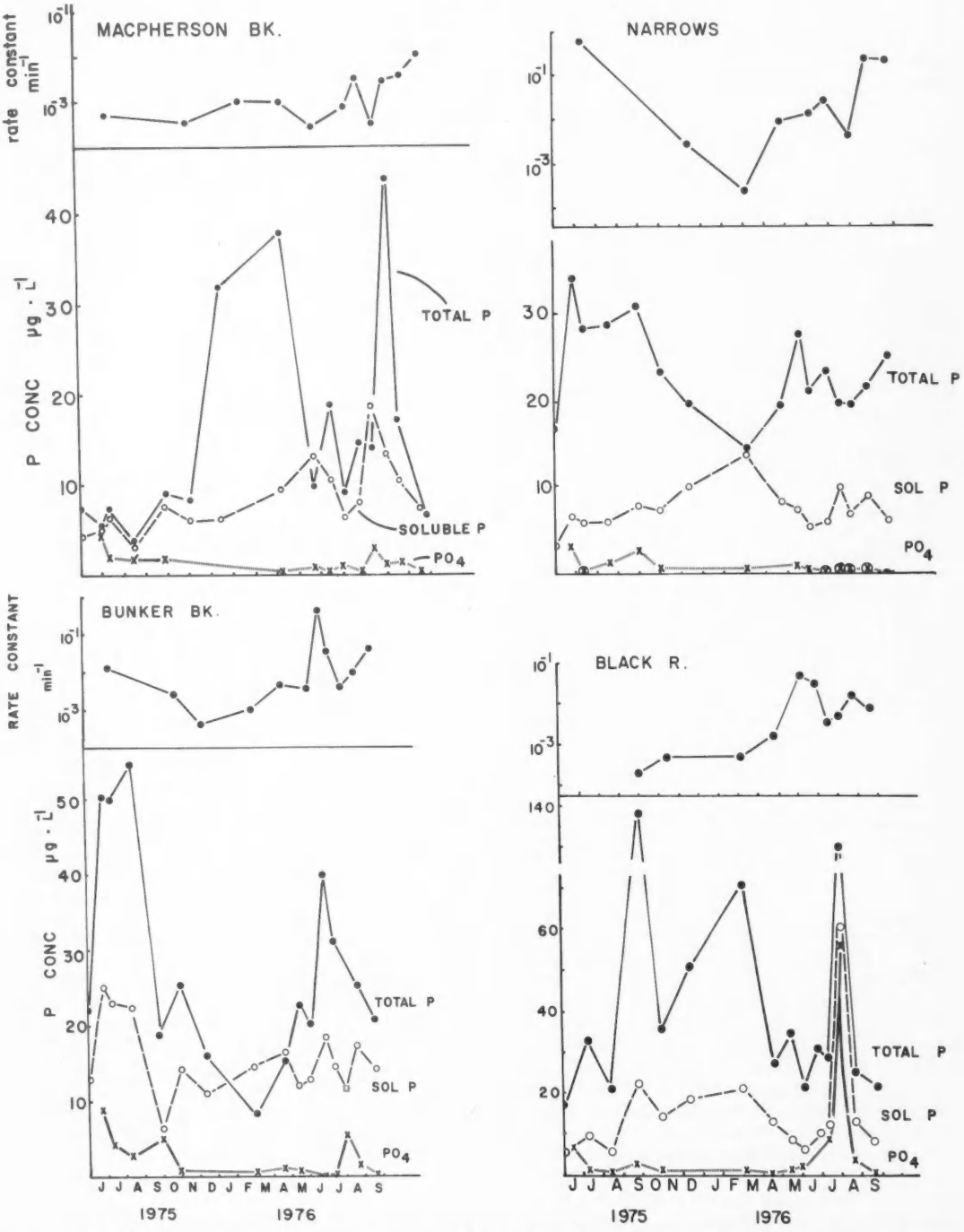

FIG. 3. Total P, soluble P, PO_4, and rate constant of PO_4 uptake in four streams entering Lake Memphremagog.

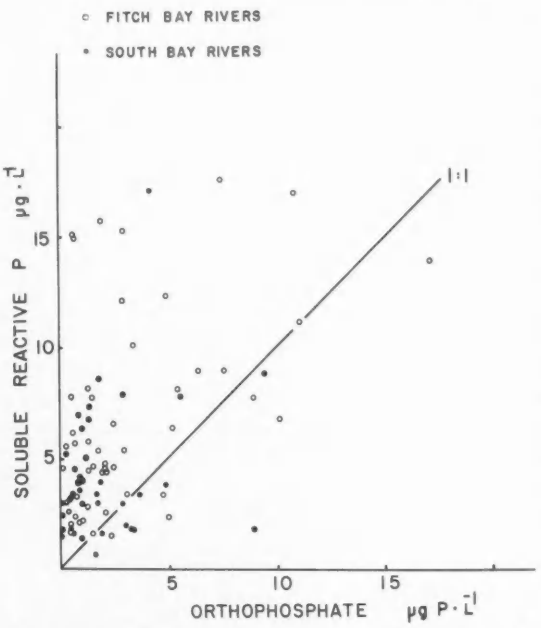

FIG. 4. Orthophosphate, plotted against soluble reactive phosphorus in water collected from all rivers, June 1975 to September 1976.

rather high level of P in the distilled water (Fig. 5) and the occasional occurrence of contaminated samples (e.g. the 300-mL sample from Fitch Creek, Fig. 5). Also, fine resolution was impossible because the volume added was large relative to the volume of gel. It was thus possible to divide the soluble phosphorus into only three coarse classes: small molecular weight P (SMWP) which eluted with the added ^{32}P-PO_4, a large molecular weight P (LMWP) which eluted at void volume, and a catchall group of intermediate fractions. These difficulties preclude detailed analysis of each date and river for relatively minor shifts in the molecular weight distribution of dissolved P. At this level of resolution, most rivers were strikingly similar: about 40% of the soluble P eluted with ^{32}P-PO_4, about 40% eluted at void volume, and the remaining 20% appeared irregularly. The most extreme rivers were the Clyde, which had a relatively high proportion of SMWP after receiving the outflow from Newport's sewage treatment plant, and Bunker Brook, the brown water of which contained a high proportion of LMWP (Table 3).

The data suggest that material similar to the limnetic colloidal P examined by Lean (1973a, b) enters the lake through its inlets. Since LMWP was not found in rainwater in the area (Peters 1977), this fraction must be formed in the soil or in the river. Groundwater analyses showed that a considerable ($\bar{x} = 35\%$) though highly variable (SD = 33) fraction of the groundwater was LMWP; most of the remainder ($62 \pm 31\%$) was SMWP (Fig. 6). However, tracer experiments (see below) showed that some of the LMWP was formed in the streams themselves. These observations are not in conflict with the engaging mechanism of colloid formation proposed by Paerl and Lean (1976), but they do broaden the potential geographical sites at which this formation may occur. Once in the lake, this large molecular weight fraction could serve as a base for the colloidal accumulation of P shown by Lean (1973a, b).

The resolution of this gel-filtration method is such that the small molecular weight fraction probably contains a number of small organic phosphates; for example, Lean's (1973a, b) x-P fraction would elute as SMWP in these analyses (D. R. S. Lean personal communication). If this is so, then the SMWP concentration should be larger than the PO_4 levels. This was, in general, observed (Fig. 7), although the uncertainties in both analyses introduced considerable variation.

The most surprising result of this investigation of P fractions was the marked similarity of the major rivers. Apparently larger rivers average any effects of spatial heterogeneity in their watersheds and in time reduce their varied effects through biological or geochemical activity in the water and sediments. The two smallest streams were exceptions: they differed from each other and from the other rivers studied. Apparently the idiosyncracies of very restricted watersheds may be expressed in their streams.

During the very dry summer of 1975 water levels were low in all streams, and MacPherson Brook was apparently reduced to base flow for average P fractions in the stream (total P = 6.7 µg/L; soluble P = 5.4 µg/L; PO_4 = 2.6 µg/L; LMWP = 40%; SMWP = 50%) and approached those of ground water (soluble P = µg/L; PO_4 = 2.2 µg/L; LMWP = 35%; SMWP = 62%). The heavy storm of September 28 had very little effect on stream flow or P fractions; instead rainwater seemed to be held in the soil. Bunker Brook rose to extremely high values in the same summer; its color deepened and its volume decreased. F. H. Rigler (unpublished data) has found a positive relation between color and P level in small streams on Dartmoor, England.

In winter, P concentration fell in Bunker Brook. Similarly, Dillon (1974) found that total P in headwater streams in central Ontario decreased during winter; all these streams contained brown water (F. H. Rigler personal communication). In MacPherson Brook the P levels rose dramatically during winter, which probably reflects increased erosion and scouring resulting from increased flow. Higher flow was maintained in both streams in 1976. Phosphorus levels remained high in MacPherson and did not reach the 1975 peaks in Bunker. Streams draining boggy areas seem to increase their P concentration at low flow, but without simultaneous flow measurements it is impossible to attribute this to increased decomposition when the water table

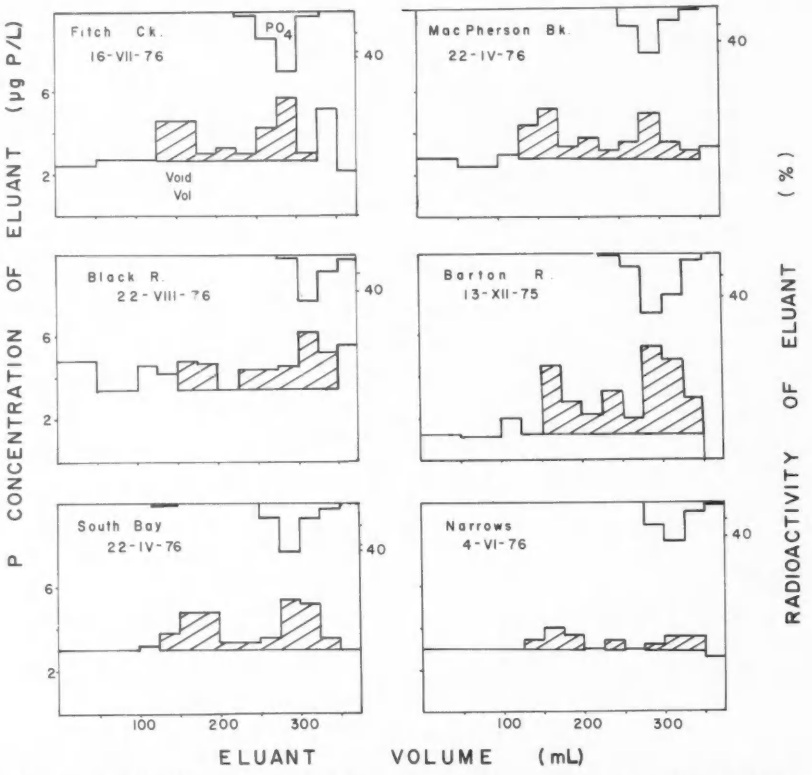

FIG. 5. Gel-filtration analyses of soluble P in water from six streams on six dates. Lower histogram in each panel shows the distribution of chemically measured P in each effluent fraction (hatched area) above the background level (clear area) of phosphorus in the eluant. Upper histogram indicates the position of a ^{32}P-PO_4 marker in each run expressed as a percentage of added tracer. The first fraction containing soluble river P appeared at void volume in all cases.

is low or simply to the concentration of a set amount of decomposition products in a diminished volume of water. Nevertheless the effect of P loading depends more on the concentration of the P load than its total quantity (Dillon 1975).

PHOSPHORUS KINETICS

In lakes it has been adequately demonstrated that the phosphorus fractions are not separate and static entities, but rather different components of an interactive system (Lean 1973a, b). If this also occurs in river waters, the presence of a small orthophosphate pool is not indicative of only a small amount of available P. Those components that are capable of exchange with orthophosphate must also be available. In the present study such compartments were identified by following the movement of ^{32}P-PO_4 from orthophosphate to the other fractions during short-term incubations.

The proportion of the observed P fractions (soluble P, LMWP, SMWP) remained constant over the course of these experiments. Assuming, then, that the system was in a steady state, any uptake of dissolved organic or particulate P must be balanced by the release of unlabeled PO_4. Thus, at least parts of the organic and particulate P fractions would be turning over and available.

Orthophosphate uptake — The turnover rate or the rate constant of PO_4 uptake by suspended material (k, in fraction per minute) followed the same seasonal pattern observed in lakes (Rigler 1964; Peters 1975a; Levine 1975): winter values were low and summer values high (Fig. 3, Table 2). However, variations in turnover rate between consecutive dates were more marked in rivers and seasonal differences were not significant in the cases of Fitch Creek and MacPherson Brook, although minima and lower average values were observed during the winter. In the other cases, winter values were significantly lower ($P > 95\%$, Mann-Whitney test, Conover 1971). The absolute values in embayments, in lake outflows (Clyde River above Newport), and in Bunker

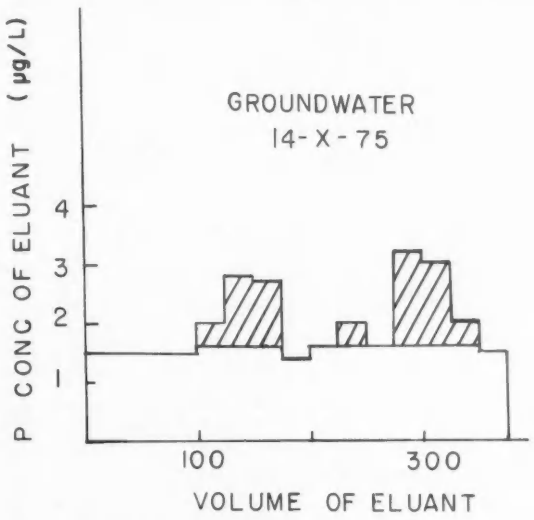

FIG. 6. Gel-filtration analysis of P in groundwater filtrate. No tracer was added to this sample.

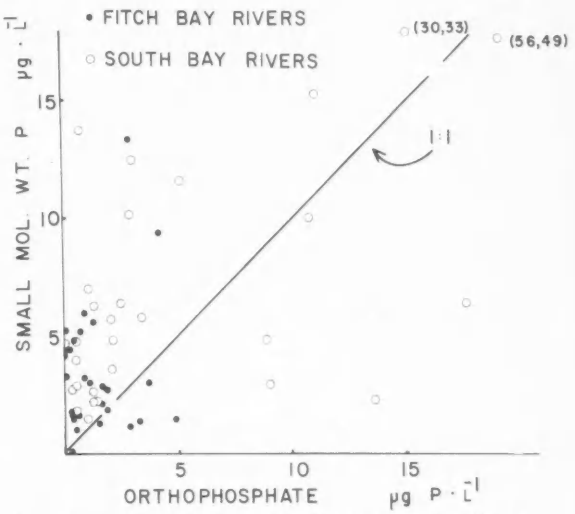

FIG. 7. Small molecular weight P plotted against PO_4 in all stream waters.

Brook were similar to those observed in lakes: k was occasionally $>0.1 \cdot min^{-1}$ (Fig. 3). In the remaining rivers the turnover rate was an order of magnitude slower. The few reported values of PO_4 uptake in streams suggest that flowing waters typically have slower rates of turnover (Rigler 1956; Ball and Hooper 1963; Hooper and Ball 1966; Halmann and Stiller 1974; Peters 1975a). In general, the seasonal cycle showed large fluctuations in turnover rate, some of which reflect rapid increases in PO_4 supply but others apparently depended upon more subtle changes in P demand of the suspended material.

In general, studies of tracer uptake in lakes have attributed the removal of ^{32}P-PO_4 from solution to biological processes (Rigler 1956; Lean and Rigler 1974) and studies with sediments have been primarily concerned with nonbiological interactions (Li et al. 1972; Hayes et al. 1952). Pomeroy et al. (1965) suggest that uptake in poisoned samples may serve to distinguish the two processes. To examine this, ^{32}P-PO_4 was added to samples of water from four sites (Black, Barton, Bunker, and South Bay) that had been collected in August 1977 and stored with chloroform for 1 mo. Rate constants of uptake were two orders of magnitude less than summer rates observed in 1975 and 1976 in the same rivers. Unfortunately, chloroform also leads to orthophosphate release (Berman 1970) and increased PO_4 concentrations would slow uptake (Fig. 1 this study; Rigler 1966). In my experiments soluble P was increased following chloroform addition and remained high; since this increased soluble P analyzed as SMWP (R. H. Peters unpublished data), there is some probability that the increase represents PO_4 release from particles. Because the slow rates of tracer incorporation in poisoned samples may indicate either the importance of biological processes in uptake or the increased competition between tracer and carrier for nonbiological sites of phosphate exchange, no attempt is made here to identify the mechanism of tracer uptake as biological or physicochemical.

On being flushed into a lake, particles that are actively engaged in exchange with their environment may release a large portion of their P by desorbtion (Li et al. 1972), decomposition (Golterman 1964; Krause 1964), or predation by zooplankton (Peters and Rigler 1973; Peters 1975b). However, low turnover rates in larger rivers suggest that not all of the particulate P is active material. If the bulk of this inactive material is an insoluble, inorganic P eroded from the watershed (e.g. apatite) it may sediment soon after entering a lake with no effect on the lake's trophic status. This appears to be the case in the Thompson River entering Kamloops Lake (St. John et al. 1976) and may explain the decrease in total P between the Barton and Black and that in South Bay. However, some inactive materials might decompose, in which case their inactivity in nutrient uptake is not a measure of unavailability. Human wastes frequently have pronounced biological effects (Edmondson 1972; Rohlich 1969) and probably this is also the case with the chlorinated sewage of Newport, which had a very low rate of orthophosphate uptake once mixed into the Clyde River.

Although a low rate of P turnover cannot be used to identify unavailable P, a high rate may suggest that the particulate P is an exchanging material that is probably available. The activity per unit of particulate P was accordingly calculated by dividing the rate constant of orthophosphate uptake at each sampling date and site by the particulate P concentration. (A further step, multiplication by the PO_4 concentration, produced no

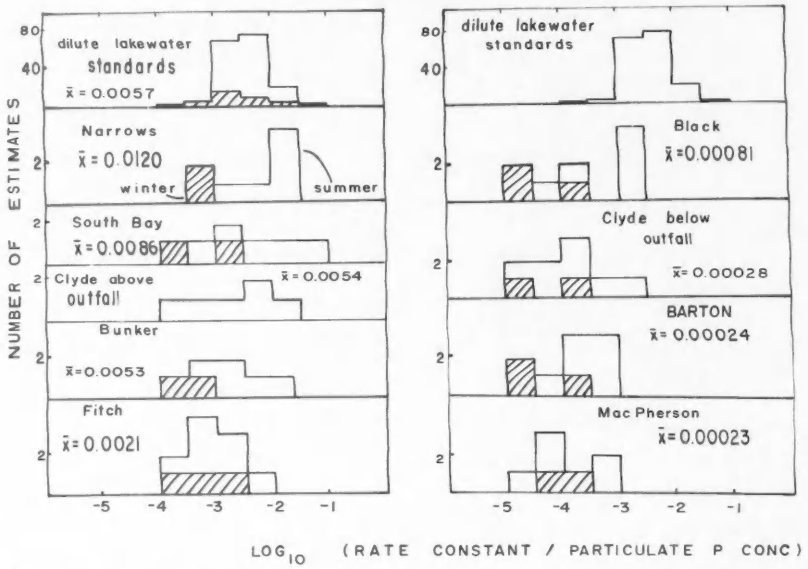

FIG. 8. Biological activity of particulate P from nine river water sites compared with that in dilute lake water. The same standard data are represented in the uppermost histograms on both sides of the figure.

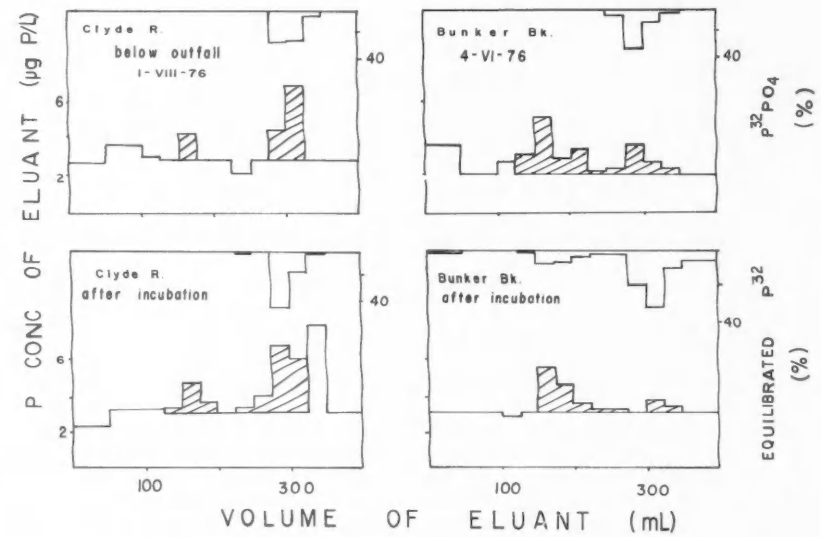

FIG. 9. The labeling of large molecular weight P by equilibration with tracer. Upper panels on both sides show the results of gel-filtration analyses of river-water filtrates with added ^{32}P-PO$_4$. Lower panels give the results of similar analyses of filtrates of whole river water that had been equilibrated with ^{32}P-PO$_4$. Bunker Brook (lower right) shows the labeling of the LMWP, whereas LMWP in the Clyde River (lower left) was not radioactive after equilibration.

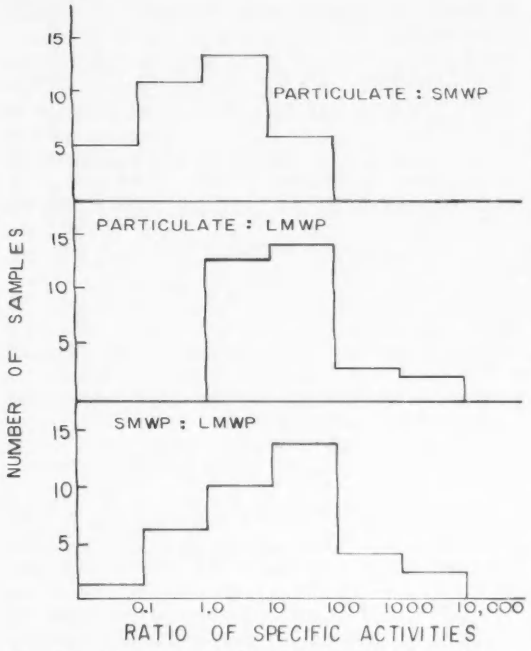

FIG. 10. Frequency distributions of the ratios of the specific activities of three P fractions at the end of short-term uptake experiments. SMWP:particulate P (upper panel); LMWP:SMWP (middle panel); and LMWP:particulate (lower panel).

change in the overall patterns, probably because multiplication compounds experimental error, and so is not included.) This index is compared with similar values calculated from the lake-water standards used in the radiological bioassay (Fig. 8). This comparison suggests that much of the particulate P in South Bay, Fitch Bay, the Clyde River above Newport, and Bunker Brook is available. Other rivers had low indices of particulate P availability, which suggests a high proportion of unavailable (probably Barton and MacPherson) or dead (probably Clyde below Newport) particulate material. Fitch Creek and Black River had intermediate values.

LMWP and SMWP — Figure 9 shows that if ^{32}P-PO_4 is incubated in whole river water, some of the tracer may appear in the large molecular weight fraction of the soluble P. This was occasionally observed at all stations but in no station repeatedly. This higher variation relative to lakes (Lean 1973a, b) is probably a function of higher PO_4 concentrations in river water plus the lower and more varied ratios of turnover rate to equilibration time in my experiments.

The phrase "equilibration time" indicates only the length of time ^{32}P-PO_4 remained in whole river water prior to filtration and does not imply that tracer equilibrium was achieved. In fact, the three major fractions, particulate P, LMWP, and SMWP, generally had different specific activities at the end of the experiment (Fig. 10). Typically, particles had the highest specific activity; but when PO_4 uptake was slow (in most winter samples and in summer in MacPherson Brook, the Black, the Barton, and the Clyde below the sewage outfall) the specific activity of the SMWP was highest. Large molecular weight P labeled slowly and usually had the lowest specific activity. However, LMWP had a higher specific activity than SMWP in samples from MacPherson in November and from the South Bay rivers in December.

The general patterns in Fig. 10 suggest that the primary exchange is between SMWP and particles, since their specific activities were similar in order of magnitude. Since the specific activity of LMWP was always less than that of particles and usually less than that of SMWP, it is probable that this material exchanges more slowly than the other two. The greater variation in the ratio of specific activities of SMWP and LMWP probably reflects a less direct interaction between these fractions. In short, the pattern of labeling of these three fractions can most easily be interpreted with Leans's (1973a, b) model of ^{32}P-PO_4 exchange in lakes. Tracer first moves to the particles from the SMWP and then a portion of the "excreted" tracer is incorporated by LMWP; the rest exchanges with SMWP.

P AVAILABILITY

Because short-term labeling experiments cannot yield quantitative estimates of the exchangeable P in particulate or soluble organic P, only PO_4 gives an unambiguous measure of P that is available to lake plankton. These data suggest that small headwater streams have a more immediate impact on downstream lakes than do rivers with more complex sources. However, the low values of PO_4 in other rivers does not indicate that only about 8% of the total P is ultimately available, for orthophosphate is only one of a series of exchanging components. The PO_4 concentration therefore provides only a minimum estimate of available P. This fraction is rapidly taken up by the plankton, as the low concentrations and rapid turnover in the two embayments show.

Figure 11 gives a hypothetical plot of total P concentration against available P. The maximum value is given by the 45° line, the minimum by the lower line, which represents 8% of the total P (the average proportion of orthophosphate measured). Each P source assumes an abscissal position determined as the mean summer concentration of total P ± 1 SE. The amount of available P was estimated from the proportion of PO_4 in each stream plus an estimate of the proportion of available particulate and dissolved organic P. For all rivers except the Clyde after Newport, a minimal estimate of available particulate P was calculated as $P_i \times B_i/B_e$ where P_i is the particulate P concentration in

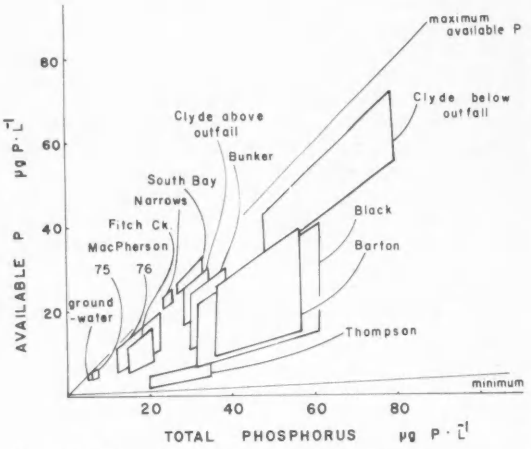

FIG. 11. Tentative biological availability in various sources for Lake Memphremagog. Data from the Thompson River (St. John et al. 1976) are included for comparison.

river i, B_i is its average summer "activity per unit of particulate P" given in Fig. 8, and B_c is the average value for this index in the two embayments, South Bay and Fitch Bay. This calculation assumes that in summer the activity per unit of active particulate P is a constant at all sites and dates and that all the particulate P in embayments is active and biologically available. The estimate of available P was further increased by assuming that up to half of the remaining particulate P was decomposing and so was also available and that between 50 and 100% of the dissolved organic P was available; these ranges give the vertical spread of the tetrahedrons in Fig. 11. The available particulate P in the Clyde below the sewage outfall was calculated as the sum of that above the outfall plus the additional particulate P added at the outfall; i.e. all of the particulate added by the sewage plant was assumed to decompose in the lake. The position of the Thompson River was also included because of its low P availability: up to 80% of total P is apatite (St. John et al. 1976). Although the scheme in Fig. 11 is hypothetical and arbitrary, it represents my tentative conceptualization of the P availability in the studied streams.

The figure suggests that variation in the impact of P loading to lakes increases with total P load, as is also apparent from the P–chlorophyll relationship of Dillon and Rigler (1974). Lakes fed by groundwater or by streams at base flow (e.g. MacPherson in 1975) will receive a low concentration of readily available P; this may explain why headwater lakes in studies by Dillon (1974) and Scheider (1975) usually had high chlorophyll to P ratios. Streams that drain one lake into another (e.g. Clyde above Newport, South Bay, and Fitch Bay) should also carry a high proportion of available P. Erosion induced by heavy runoff (e.g. MacPherson in 1976) or development in the watershed (e.g. Barton, Fitch, Black) may increase the amount of unavailable P and the uncertainty in estimation of biological impact on the lake. Rivers carrying domestic wastes (e.g. Clyde below Newport) may have the greatest effect of all sources because of their high concentrations and possibly high availabilities. This figure reveals an interesting discrepancy in that only the highest estimates of available P in the Barton and the Black could supply the available P concentration in South Bay. This suggests either that the assumption that all particulate P in embayments and lakes is available is incorrect or that a high proportion of the P in those rivers is available. More importantly, Fig. 11 suggests that the most significant work, in terms of reducing our uncertainty, is to be done on rivers containing relatively high P concentrations. These hypotheses will serve to restrict and focus the aims of further research.

Conclusions

Although total P differed among the nine sites sampled, its distribution among the fractions studied was very similar. Approximately one third of the phosphorus passed through a 0.45-μm filter. This "soluble" P consists of about 40% large molecular weight P ($>$ 5000 mol wt) and 40% small molecular weight P ($<$ 400 mol wt); the remainder appeared irregularly as intermediate fractions. Orthophosphate formed 8% of the total P but showed no consistent relation to soluble reactive P.

Experiments with radioactive tracers showed that all fractions were involved in exchange with orthophosphate and therefore were, in part, available. Future work should attempt to quantify the amounts of available P in rivers with relatively high P concentrations.

Acknowledgments

I sincerely thank R. Carlson, A. Cattaneo, J. Kalff, W. Leggett, K. Webster, and the other members of the Lake Memphremagog project. Funds were provided by the Inland Waters Directorate of Fisheries and the Environment Canada, the Department of Education of the Province of Quebec, the National Research Council of Canada and the Faculty of Graduate Studies and Research, McGill University. The Memphremagog project is deeply indebted to the late Mr J. Routledge of Belmere Farm, whose generosity and kind hospitality made our work far easier.

AHL, T. 1972. Plant nutrients in Swedish lake and river waters. Verh. Int. Ver. Limnol. 18: 362–369.

BALL, R. C., AND F. F. HOOPER. 1963. Translocation of phosphorus in a trout stream ecosystem, p. 217–228. *In* V. Schultz and A. W. Klement [ed.] Proc. 1st Symp. Radioecol. Rheinhold, New York.

BARBANTI, L., A. CALDERONE, AND A. CAROLLO. 1974. Indagini Idrologiche e Chimiche dei Principali Tributari Piemontesi del Lago Maggiore in relazione alle sue condificazioni trofiche. Ist. Ital. di Idrobiol. Verbania. 149 p.

BERMAN, T. 1970. Alkaline phosphatases and phosphorus availability in Lake Kinneret. Limnol. Oceanogr. 15: 663–674.

CHAMBERLAIN, W. 1968. A preliminary investigation of the nature and importance of soluble organic phosphorus in the phosphorus cycle of lakes. Ph.D. Thesis. Univ. Toronto, Toronto, Ont. 165 p.

CONOVER, W. J. 1971. Practical nonparametric statistics. John Wiley and Sons, Inc., New York, N.Y. 462 p.

DILLON, P. J. 1974. The prediction of phosphorus and chlorophyll concentrations in lakes. Ph.D. Thesis. Univ. Toronto, Toronto, Ont. 330 p.

1975. The phosphorus budget of Cameron Lake, Ontario: the importance of flushing rate to the degree of eutrophy of lakes. Limnol. Oceanogr. 20: 28–39.

DILLON, P. J., AND F. H. RIGLER. 1974. The phosphorus–chlorophyll relationship in lakes. Limnol. Oceanogr. 19: 767–773.

EDMONDSON, W. T. 1972. Nutrients and phytoplankton in Lake Washington, p. 172–193. *In* G. E. Likens [ed.] Nutrients and eutrophication. The limiting nutrient controversy, Vol. I. Am. Soc. Limnol. Oceanogr. Spec. Symp.

FERRANTE, J. G. 1976. The characterization of phosphorus excretion products of a natural population of limnetic zooplankton. Hydrobiologia 50: 11–15.

GOLTERMAN, H. L. 1964. Mineralization of algae under sterile conditions or by bacterial breakdown. Verh. Int. Ver. Limnol. 15: 544–548.

1973. Natural phosphate sources in relation to phosphate budgets: a contribution to the understanding of eutrophication. Water Res. 7: 3–18.

HALMANN, M., AND M. STILLER. 1974. Turnover and uptake of dissolved phosphate in freshwater. A study in Lake Kinneret. Limnol. Oceanogr. 19: 774–783.

HARTLAND-ROWE, R., AND P. B. WRIGHT. 1975. Effects of sewage effluent on a swampland stream. Verh. Int. Ver. Limnol. 19: 1575–1583.

HAYES, F. R., J. A. MCCARTER, M. L. CAMERON, AND D. A. LIVINGSTONE. 1952. On the kinetics of phosphorus exchange in lakes. J. Ecol. 40: 202–212.

HERON, J. 1962. Determination of phosphorus in water after storage in polyethylene. Limnol. Oceanogr. 7: 316–321.

HOBBIE, J. E., AND G. E. LIKENS. 1973. Output of phosphorus, dissolved organic carbon and fine particulate carbon from Hubbard Brook watersheds. Limnol. Oceanogr. 18: 734–742.

HOOPER, F. F., AND R. C. BALL. 1966. Bacterial transport of phosphorus in a stream ecosystem, p. 535–549. *In* Disposal of radioactive wastes into seas, oceans and surface waters. IAEA, Vienna.

KLAUSNER, S. D., P. J. ZWERMAN, AND D. F. ELLIS. 1974. Surface runoff losses of soluble nitrogen and phosphorus under two systems of soil management. J. Environ. Qual. 3: 42–46.

KRAUSE, H. R. 1964. Zur Chemie und Biochemie der Zersetzung von Susswasserorganismen unter besonder Berucksichtungen des Abbaues der organischen Phosphorkomponenten. Verh. Int. Ver. Limnol. 15: 549–561.

LEAN, D. R. S. 1973a. Phosphorus dynamics in lake water. Science 179: 678–680.

1973b. Movements of phosphorus between its biologically important forms in lake water. J. Fish. Res. Board Can. 30: 1525–1536.

1976. Phosphorus kinetics in lake water: influence of membrane pore size and low pressure filtration. J. Fish. Res. Board Can. 33: 2800–2804.

LEAN, D. R. S., AND F. H. RIGLER. 1974. A test of the hypothesis that abiotic complexing influences phosphorus kinetics in epilimnetic lake water. Limnol. Oceanogr. 19: 784–788.

LEVINE, S. 1975. Orthophosphate concentration and flux within the epilimnia of two Canadian Shield lakes. Verh. Int. Ver. Limnol. 19: 624–629.

LI, W. C., D. E. ARMSTRONG, J. D. H. WILLIAMS, R. F. HARRIS, AND J. K. SYERS. 1972. Rate and extent of inorganic phosphate exchange in lake sediments. Soil Sci. Am. Proc. 36: 279–285.

MENZEL, D. W., AND N. CORWIN. 1965. The measurement of total phosphorus in seawater based on the liberation of organically bound fractions by persulphate oxidation. Limnol. Oceanogr. 10: 280–282.

MINEAR, R. A. 1972. Characterization of naturally occurring organophosphorus compounds. Environ. Sci. Technol. 6: 431–437.

NUMANN, W. 1967. Veranderungen der Phosphor Last in einen Flusslauf gezeigt am Bodenseezufluss Argen. Gas Wasserfach. 30: 833–834.

1968. Das Verhalten von organischer fracht, Phosphor-und Stickstoffverbindugen in einem Flusslauf nach Eintrag durch hausliche und industrielle Abwässer sowie durch landwirtschaftliche Düngung (Bodenseezufluss, Schussen). Arch. Hydrobiol. 64: 377–399.

ONGLEY, E. D. 1976. Sediment yields and nutrient loadings from Canadian watersheds tributary to Lake Erie: an overview. J. Fish. Res. Board Can. 33: 471–484.

PAERL, H. W., AND D. R. S. LEAN. 1976. Visual observations of phosphorus movement between algae, bacteria, and abiotic particles in lake waters. J. Fish. Res. Board Can. 33: 2805–2813.

PETERS, R. H. 1975a. Orthophosphate turnover in central European lakes. Mem. Ist. Ital. Idrobiol. Dott Marco de Marchi Pallanza Italy 32: 297–311.

1975b. Phosphorus regeneration by natural populations of limnetic zooplankton. Verh. Int. Ver. Limnol. 19: 273–279.

1977. Availability of atmospheric orthophosphate. J. Fish. Res. Board Can. 34: 918–924.

PETERS, R. H., AND D. R. S. LEAN. 1973. The characterization of soluble phosphorus released by limnetic zooplankton. Limnol. Oceanogr. 18: 270–279.

PETERS, R. H., AND S. MACINTYRE. 1976. Orthophosphate turnover in East African Lakes. Oecologia 25: 313–319.

PETERS, R. H., AND F. H. RIGLER. 1973. Phosphorus regeneration by *Daphnia*. Limnol. Oceanogr. 18: 821–839.

POMEROY, L. R., E. E. SMITH, AND C. M. GRANT. 1965. The exchange of phosphate between estuarine water and sediments. Limnol. Oceanogr. 10: 167–172.

RICH, P. H., AND B. L. PALOTTI. 1977. Potential contribution of atmospheric fallout to the phosphorus budget of Columbia Lake, Connecticut. J. Fish. Res. Board Can. 34: 692–697.

RIGGS, D. S. 1970. The mathematical approach to physiological problems. The M.I.T. Press, Cambridge, Mass. 445 p.

RIGLER, F. H. 1956. A tracer study of the phosphorus cycle in lakewater. Ecology 37: 550–562.

1964. The phosphorus fractions and the turnover

time of inorganic phosphorus in different types of lakes. Limnol. Oceanogr. 9: 511–518.

1966. Radiobiological analysis of inorganic phosphorus in lake water. Verh. Int. Ver. Limnol. 15: 465–470.

1968. Further observations inconsistent with the hypothesis that the molybdenum blue method measures inorganic phosphorus in lake water. Limnol. Oceanogr. 13: 7–13.

1973. A dynamic view of the phosphorus cycle in lakes, p. 539–572. *In* E. J. Griffith, A. Beeton, J. M. Spencer, and D. T. Mitchell [ed.] The environmental phosphorus handbook. John Wiley and Sons, Inc., New York, N.Y.

ROHLICH, G. A. 1969. Engineering aspects of nutrient removal, p. 371–382. *In* Eutrophication: Causes, consequences, correctives. Natl. Acad. Sci.

ST. JOHN, B. E., E. C. CARMACK, R. J. DALEY, C. B. J. GRAY, AND C. H. PHARO. 1976. The limnology of Kamloops Lake. Dep. Environ. Inland Waters Directorate, Pacific and Yukon Region, Vancouver, 167 p.

SCHEIDER, W. A. 1975. The prediction of phosphorus and chlorophyll in small Shield lakes. M.Sc. Thesis. Univ. Toronto, Toronto, Ont. 129 p.

SCHINDLER, D. W. S., H. KLING, R. V. SCHMIDT, J. PROKOPOWICH, J. E. FROST, R. A. REID, AND M. CAPEL. 1973. Eutrophication of Lake 227 by addition of phosphate and nitrate: the second, third and fourth years of enrichment, 1970, 1971 and 1972. J. Fish. Res. Board Can. 30: 1415–1440.

STRICKLAND, J. D. H., AND T. R. PARSONS. 1968. A practical handbook of seawater analysis, 2nd ed. Bull. Fish. Res. Board Can. 167: 331 p.

UNGER, U. 1969. Die Wasserqualität der Donau von der Bregquelle bis oberhalb Ulm. Arch. Hydrobiol. Suppl. 36: 45–60.

WALTON, C. P., AND G. F. LEE. 1972. A biological evaluation of the molybdenum blue method for orthophosphate analysis. Verh. Int. Ver. Limnol. 18: 676–684.

WILLIAMS, J. D. H., J. M. JAQUET, AND R. L. THOMAS. 1976. Forms of phosphorus in the surficial sediments of Lake Erie. J. Fish. Res. Board Can. 33: 413–429.

Feeding Response of Atlantic Salmon (*Salmo salar*) Alevins in Flowing and Still Water[1]

D. M. RIMMER[2] AND G. POWER[3]

Department of Biology, University of Waterloo, Waterloo, Ont.

RIMMER, D. M., AND G. POWER. 1978. Feeding response of Atlantic salmon (*Salmo salar*) alevins in flowing and still water. J. Fish. Res. Board Can. 35: 329–332.

Atlantic salmon (*Salmo salar*) alevins presented with lake zooplankton in still water readily consumed prey items, but only if the prey were nearby and moving. Feeding was initiated from the bottom or from midwater, but no search or pursuit behavior was noted. Stomach analyses of alevins exposed to lake zooplankton assemblages for 3 h in still and flowing (7.2 $cm \cdot s^{-1}$) water revealed that the two groups consumed similar diets, but that the still-water group had a greater total food consumption. We conclude that for alevins to feed successfully, food need not be carried in a water current, but that motion of the prey is necessary. This motion can be provided by water current or by the prey. The role of prey motility in the feeding of young salmonids is briefly discussed.

Key words: Atlantic salmon, alevins, feeding, water current

RIMMER, D. M., AND G. POWER. 1978. Feeding response of Atlantic salmon (*Salmo salar*) alevins in flowing and still water. J. Fish. Res. Board Can. 35: 329–332.

Des alevins de saumon atlantique (*Salmo salar*) auxquels on offre du zooplancton de lac dans une eau morte consument volontiers les proies, mais seulement si ces dernières sont proches et en mouvement. L'alimentation est déclenchée au fond ou entre deux eaux, mais nous n'avons observé aucun comportement de recherche ou de poursuite. L'analyse des contenus stomacaux d'alevins exposés à du zooplancton de lac pendant 3 h dans de l'eau morte et de l'eau courante (7.2 $cm \cdot s^{-1}$) démontre que les deux groupes consomment les mêmes proies, mais que le groupe maintenu en eau morte consomme un plus grand volume de nourriture. Nous concluons que la nourriture, pour que les alevins se nourrissent avec succès, ne doive pas nécessairement être transportée par le courant, mais qu'elle doive être en mouvement. Ce mouvement peut être causé par le courant ou par les proies. Nous analysons brièvement le rôle de la mobilité des proies dans l'alimentation des jeunes salmonidés.

Received June 1, 1977
Accepted December 1, 1977

Reçu le 1 juin 1977
Accepté le 1 décembre 1977

HATCHERY-REARED Atlantic salmon (*Salmo salar*) alevins were planted in four originally fishless lakes of the Matamek River system, Québec (Power et al. 1973), during 1970–74 in an attempt to supplement the natural smolt production of the Matamek River. Investigations during 1973–74 revealed poor survival and this was attributed to high alevin mortality (Rimmer 1975).

In nature, the period following the absorption of the yolk sac and the emergence from the gravel is one of high mortality, attributable to starvation, predation, and competition for space (Mills 1971). In some species such mortality has been associated with a lack of suitable food after external feeding begins (Bagenal and Braum 1971). The feeding of young salmonids in streams is restricted largely to drift organisms (Nilsson 1957; Kalleberg 1958). It has been stated that young salmonids will feed on only those items that are in motion in a water current (Stuart 1953; Jones 1959; Mundie 1969; Protasov 1970). In goldfish (*Carassius auratus*) the retina functions as a peripheral filter for motion stimuli in that it possesses numerous directionally sensitive units, most of which respond best to spots moving along the horizontal axis. Of these units the majority respond to nasalward, rather than to temporalward, movements (Ingle 1968).

Thus, we hypothesized that the frontal approach of potential food items may be important in eliciting a

[1]Contribution No. 28 from the Matamek Research Station, Sept-Îles, Qué.

[2]Present address: Department of Biology, University of New Brunswick, Fredericton, N.B. E3B 5A3.

[3]Present address: Centre d'Etudes Nordiques, Université Laval, Québec, Qué. G1K 7P4.

Printed in Canada (J4860)
Imprimé au Canada (J4860)

feeding response in alevins and that the lack of water current in a lentic environment may have contributed significantly to the high mortality suffered by the alevins in the Matamek lakes study. This note reports on an experiment designed to test this hypothesis.

Materials and methods — Alevins (*sensu* Balon 1975) used in this study were produced at the Provincial Fish Hatchery located at Tadoussac, Québec, and originated from brood stock captured in the Saguenay River estuary. Eggs were incubated under a natural temperature regime and hatching occurred during April 1974 after which the fish were reared in hatchery flumes. At the time of the experiment on July 2, 1974, they had a mean fork length of 25.1 mm and had been fed for 2 wk on dry hatchery food and minced beef heart–liver. The alevins were transported to the Matamek Research Station, 450 km northeast of Tadoussac, where the experiment was performed.

Preliminary observations were made of alevin responses to lake zooplankton in still water. Twenty-five fish were placed into each of three clear plastic pans ($45 \times 22 \times 15$ cm) which were shielded on three sides from outside activity. Each pan contained a layer of clean gravel overlain by 7.5 cm of filtered lake water which was periodically aerated with a hand pump. The alevins were starved for 24 h after which a mixture of lake zooplankton was introduced into their pan. The behavior of the alevins was observed for 120 min. This was repeated for each pan.

To investigate the role of water current in feeding, six identical testing channels were made with green circular plastic wash tubs. A tub of 38 cm diam was fitted with a central core consisting of a 15-cm diam plastic cylinder. This created an annular channel 11.5 cm wide and 128 cm in midchannel circumference. Eight holes were cut in the central cylinder at equal intervals around the circumference, 6 cm from the bottom. This allowed the maintenance of a constant water depth of 6 cm in the channels, the overflow passing through the holes in the central cylinder and out of the device through a central hole in the bottom.

To produce a current, a length of rubber hose of 1 cm inside diameter was fitted at one end with a 2.27-L tinplate funnel. The other end of the hose was wired obliquely along the inside outer wall of the channel. The tub construction was placed on a rock shelf beside a waterfall that fell directly from the outlet of the lake and the funnel was fixed in the stream of running water. Number 10 plankton netting was placed over the funnel mouth and the exit ports to prevent the entrance and exit of food organisms. The channel bottom was left bare. In this way, an artificial flow-through stream 6 cm deep was created and the water current velocity in the channel could be controlled by a screw clamp on the hose. The clamps were set so that three channels had no perceptible current, although a slight exchange of water was allowed; the other three channels had currents of similar velocity, averaging 7.2 ± 0.9 cm·s^{-1}, sufficient to carry zooplankton.

After arrival at the field camp, 150 alevins were allowed to recover from transport for 2 days without feeding. Twenty-five alevins were then placed into each of the six channels. After a 1-h acclimation period each channel was inoculated with equal volumes of food concentrate consisting of live zooplankton from the lake. The zooplankton assemblages presented to each channel were subsamples of a large single collection and were therefore assumed to be qualitatively and quantitatively comparable. The food concentrate contained the following families: Bosminidae, Chaoboridae larvae, Cyclopidae, Daphnidae, Holopedidae, Polyphemidae, and Sididae. The alevins were allowed access to these organisms for 3 h, after which they were killed and preserved whole in 5% formalin. Stomach contents were later removed, identified, and sorted into families. The diet of each test group was described by the points method (Hynes 1950). A full stomach was allotted 25 points. The points gained by each family (scored to the nearest point) in individual alevins of each replicate were summed so that the data represented the accumulated points for groups of 25 fish. The differences between the mean points accumulated by each zooplankton family and the total amount of food consumed in still and flowing water were tested with one-way analyses of variance at a 5% significance level.

Results — Our preliminary observations revealed that alevins recognized natural lake zooplankton as food and readily captured and ingested them in still water. This was done from stationary positions, either at middepth or from the bottom. Alevins darted only toward prey that were nearby and in motion directly in front of them. They ignored stationary prey, even when close. Alevins did not appear to search actively for prey or to pursue them after unsuccessful attempts at capture. No preference for any of the prey species was evident.

In fish from the stream channels 90% of all stomachs were filled to distension regardless of whether the fish were in still or flowing water (Table 1). Neither group utilized the Holopedidae or the Cyclopidae, but both groups consumed all the other zooplankton families. The only significant difference in the amount of each food item ingested occurred in the Daphnidae, which were ingested in greater amounts in still water. Also, there was a significant difference in the total amount of food ingested by the two test groups, the still-water fish consuming more food than the flowing-water fish.

Discussion — The attack behavior observed in our preliminary observations is very similar to that noted by Stuart (1953). Naive alevins readily recognized novel food items because they attacked these prey without apparent hesitation. Jenkins et al. (1970) reported that inexperienced hatchery-reared rainbow trout (*S. gairdneri*) adjusted rapidly to new environments, preying on aerial and benthic invertebrates 24 h a day.

Information on the feeding behavior of Atlantic salmon alevins is scarce. Kalleberg (1958) quotes Norback (1884 — not seen by author and not cited in references) as saying that young salmon alevins stay in the substrate and are constantly supplied with crustaceans by the water current and eddies. The present results indicate that if alevins have no choice between still and flowing water, they can feed at least as well and perhaps better in still water.

Salmonids are obligate visual feeders (Protasov 1970; Ware 1972), their feeding behavior being released by the physical characteristics of their prey. Although some species of fish discriminate between prey organisms on the basis of body size, shape, and color (Kislalioglu and Gibson 1976; O'Brien et al. 1976), there appears to be

TABLE 1. Accumulated points and mean points accorded to various food items in the diets of 25 Atlantic salmon alevins held in each of still (S) and flowing (Fl) water (three replicates each), and the significance of dietary differences (analysis of variance). Diet analysis by the points method (Hynes 1950). Standard deviations are in parentheses; *significant at $\alpha = 0.05$.

Food item (family)	Replicates 1 S	1 Fl	2 S	2 Fl	3 S	3 Fl	Mean points S	Mean points Fl	F	df	P
Polyphemidae	34	23	30	32	33	28	32.3 (2.1)	27.7 (4.5)	1.54	1, 2	0.34
Daphnidae	98	76	93	74	98	68	96.3 (2.9)	72.7 (4.2)	51.97	1, 2	0.02*
Sididae	55	52	60	70	47	39	54.0 (6.6)	53.7 (15.6)	0.004	1, 2	0.96
Bosminidae	17	23	29	31	17	27	21.0 (6.9)	27.0 (4.0)	6.75	1, 2	0.12
Chaoboridae larvae	122	89	139	94	99	88	120.0 (20.1)	90.0 (3.2)	8.88	1, 2	0.10
Total	326	263	351	301	294	250	323.7 (28.6)	271.3 (26.5)	87.10	1, 2	0.01*
n	25	25	25	25	25	25					

no convincing evidence that young Atlantic salmon do so. In fact, alevins of the brown trout (*S. trutta*) and Atlantic salmon are indiscriminant in the prey items they attack, even capturing moving pieces of debris and rejecting them shortly after (Stuart 1953). Although many factors are probably involved in releasing feeding behavior in alevins, prey motility seems to be one of major importance. Several studies imply that this motion is provided by the water current in which the prey is carried. Young coho salmon (*Oncorhynchus kisutch*) eat moving objects and do not appear to take stationary items off the substrate, but if they disturb the sediment with their body movements they will attack items brought into suspension (Mundie 1969). In a stream tank, Kalleberg (1958) found that Atlantic salmon and brown trout parr were almost exclusively intent on current-borne prey, regardless of its origin. Stuart (1953) discovered that if Atlantic salmon and brown trout alevins were offered inanimate food, they would attack only those particles falling slowly through the water. Particles reaching the bottom were ignored unless they were put back into motion. Peterson (1973) states that in hatcheries Atlantic salmon alevins prefer to take artificial food floating in the water current of their tanks, but learn to take particles bouncing along the bottom.

Although the present results indicate that water current is unnecessary for successful feeding to occur, this does not mean that prey motility is not important. The motion of the prey organism is probably a strong stimulus regardless of whether the prey is spatially displaced or not. It is reasonable to assume that to a visual predator any organism will become more visible if it moves. The prey organisms used in the present experiment are all active forms exhibiting distinct jerking motions, and hence, even in still water they could provide adequate visual stimulation to elicit predatory responses from the fish. Prey activity alone may be sufficient to elicit successful feeding. For example, young sockeye salmon (*O. nerka*) enter lakes very soon after emergence and feed on zooplankton in a still-water environment (McCart 1967).

Prey motility need not be great to elicit feeding behavior from young salmon. Stuart (1953) gave Atlantic salmon and brown trout alevins a choice between live and dead mayfly nymphs (*Leptophlebia* spp.) on the bottom of an aquarium. The live nymphs remained motionless and indistinguishable from the dead ones except for intermittent vibrations of their gill lamellae; alevins readily attacked the live nymphs, but ignored the dead ones.

Our preliminary observation that alevins ignored a nearby prey organism while it was motionless, but attacked it once the prey moved, suggests that motion is necessary. The unimpaired feeding ability of alevins in still water shown here could be explained by postulating that stimulation provided by active movement of the prey organism in still water is not less than that provided by passive motion in a water current. We conclude that mortality of naive Atlantic salmon alevins newly planted in still water cannot be attributed to starvation caused by an inability to feed successfully in nonflowing water, provided the prey organisms are active in some way.

Acknowledgments—This study was financed by the Woods Hole Oceanographic Institution and the University of Waterloo. Le Ministère du Tourisme, de la Chasse et de la Pêche du Québec kindly provided the salmon alevins. We

thank Mr G. Lacroix for field assistance, Mr R. Chengaleth for taxonomic assistance, and Dr J. J. Dodson for reading the manuscript.

BAGENAL, T. B., AND E. BRAUM. 1971. Eggs and early life history, p. 116–198. *In* W. E. Ricker [ed.] Methods for assessment of fish production in fresh waters. Blackwell Scientific Publications, Oxford.

BALON, E. K. 1975. Terminology of intervals in fish development. J. Fish. Res. Board Can. 32: 1663–1670.

HYNES, H. B. N. 1950. The food of fresh-water sticklebacks (*Gasterosteus aculeatus* and *Pygosteus pungitius*), with a review of methods used in studies of the food of fish. J. Anim. Ecol. 19: 36–58.

INGLE, D. 1968. Spatial dimensions of vision in fish, p. 51–59. *In* D. Ingle [ed.] The central nervous system and fish behavior. University of Chicago Press, Chicago, Ill.

JENKINS, T. M. JR., C. R. FELDMUTH, AND G. V. ELLIOT. 1970. Feeding of rainbow trout (*Salmo gairdneri*) in relation to abundance of drifting invertebrates in a mountain stream. J. Fish. Res. Board Can. 28: 2356–2361.

JONES, J. W. 1959. The salmon. William Collins Sons and Co., Ltd., London. 192 p.

KALLEBERG, H. 1958. Observations in a stream tank of territoriality and competition in juvenile salmon and trout (*Salmo salar* L. and *S. trutta* L.). Rep. Inst. Freshwater Res. Drottningholm 30: 55–98.

KISLALIOGLU, M., AND R. N. GIBSON. 1976. Some factors governing prey selection by the 15-spined stickleback, *Spinachia spinschia* (L.). J. Exp. Mar. Biol. Ecol. 25: 159–169.

MCCART, P. 1967. Behavior and ecology of sockeye salmon fry in the Babine River. J. Fish. Res. Board Can. 24: 375–428.

MILLS, D. 1971. Salmon and trout. Oliver and Boyd, Edinburgh. 351 p.

MUNDIE, J. H. 1969. Ecological implications of the diet of juvenile coho in streams, p. 135–152. *In* T. G. Northcote [ed.] Symposium on salmon and trout in streams. H. R. MacMillan Lectures in Fisheries, Univ. British Columbia, Vancouver, B.C.

NILSSON, N.-A. 1957. On the feeding habits of trout in a stream of northern Sweden. Rep. Inst. Freshwater Res. Drottningholm 38: 154–166.

O'BRIEN, W. J., N. A. SLADE, AND G. L. Vinyard. 1976. Apparent size as the determinant of prey selection by bluegill sunfish (*Lepomis macrochirus*). Ecology 57: 1304–1310.

PETERSON, H. H. 1973. Smolt rearing methods, equipment and techniques used successfully in Sweden. Int. Atl. Salmon Found. Spec. Publ. Ser. 2: 32–62.

POWER, G., G. F. POPE, AND B. W. COAD. 1973. Postglacial colonization of the Matamek River, Quebec, by fishes. J. Fish. Res. Board Can. 30: 1586–1589.

PROTASOV, V. R. 1970. Vision and near orientation of fish. (Transl. by Israel Program for Sci. Transl., Jerusalem) 175 p.

RIMMER, D. M. 1975. Rearing Atlantic salmon (*Salmo salar* L.) in fishless lakes of the Matamek River system, Quebec. M.Sc. Thesis. Univ. Waterloo, Waterloo, Ont. 204 p.

STUART, T. A. 1953. Spawning migration, reproduction and young stages of loch trout (*Salmo trutta* L.). Freshwater Salmon Fish. Res. 5: 39 p.

WARE, D. M. 1972. Predation by rainbow trout (*Salmo gairdneri*): the influence of hunger, prey density, and prey size. J. Fish. Res. Board Can. 29: 1193–1201.

Comparison of Two Methods Used by Divers for Sampling Benthic Invertebrates in Deep Rivers

CHARLES F. RABENI[1] AND K. ELIZABETH GIBBS

Department of Entomology, University of Maine, Orono, Maine 04473, USA

RABENI, C. F., AND K. E. GIBBS. 1978. Comparison of two methods used by divers for sampling benthic invertebrates in deep rivers. J. Fish. Res. Board Can. 35: 332–336.

A modified Hess sampler was developed to estimate standing crop and was compared with rock-filled basket samplers. The baskets, although biased for some invertebrates, consistently collected more individuals and taxa. Both methods showed high efficiency, as measured by the coefficient of variation, which generally decreased with increasing pollution. The relative proportions of each invertebrate group collected by each method were similar in many instances and each method was shown to be appropriate in deep-water situations, depending upon the goal of the study.

Key words: invertebrate, sampling, river, artificial substrates, divers

[1]Present address: Center of Environmental Science, Unity College, Unity, Maine 04988, USA.

Printed in Canada (J4882)
Imprimé au Canada (J4882)

RABENI, C. F., AND K. E. GIBBS. 1978. Comparison of two methods used by divers for sampling benthic invertebrates in deep rivers. J. Fish. Res. Board Can. 35: 332–336.

Les auteurs ont mis au point un échantillonneur de Hess modifié servant à estimer la biomasse et ils le comparent avec des échantillonneurs à paniers remplis de roches. Bien que favorisant certains invertébrés, les paniers cueillent uniformément plus d'individus et de taxons. Les deux méthodes s'avèrent hautement efficaces, comme l'indique le coefficient de variation qui diminue généralement à mesure qu'augmente la pollution. Les proportions relatives de chaque groupe d'invertébrés récoltés par l'une et l'autre méthode sont semblables dans plusieurs cas. Selon le but de l'étude, chaque méthode se prête bien à un échantillonnage en eau profonde.

Received June 14, 1977
Accepted December 8, 1977

Reçu le 14 juin 1977
Accepté le 8 décembre 1977

THE recent increase in use of benthic invertebrates in water quality studies has necessitated an increase in sampling of many of the larger, deeper rivers receiving industrial and municipal effluents. Even under ideal conditions sampling stream invertebrates is notoriously inefficient and unreliable, and the problems are compounded when dealing with deep or fast-flowing rivers (Anderson and Mason 1968). Once water depths exceed a metre, standard sampling techniques, such as kick nets, Surber samplers, or dredges, are difficult or impossible to use.

A new methodology to deal with deep rivers has developed in the last few years and it has concentrated primarily upon the use of artificial substrates (Weber 1973). Most popular is the rock-filled basket which is suspended in the water from buoys, bridge abutments, or piers (Mason et al. 1970). The efficiency of this method has been demonstrated (Benfield et al. 1974; Crossman and Cairns 1974; Anderson and Mason 1968) but two problems exist: loss of organisms during retrieval of the sampler and the fact that the sampler usually does not collect organisms on the river substratum, where the effects of certain pollutants, most notably settleable solids, are most pronounced. The use of divers in deep rivers to work directly on the bottom is a way to overcome these deficiencies and has been gaining wider use (Gale and Thompson 1974a, b). This paper compares the usefulness of two sampling methods that were used by divers in a deep river.

Materials and methods — Data for this analysis were collected as part of an investigation of the benthic invertebrate communities of the Penobscot River, Maine, in July 1974. Sampling locations and pertinent environmental data are described by Rabeni (1977).

Four sites representing a gradient of water quality were sampled by two methods. The pristine site was located upstream from major habitation. The enriched site was in an area influenced by runoff from agriculture and low-density habitation. The polluted area was downstream from a municipality and paper mill where the river had begun to recover from the effects of the effluents. The highly polluted site was directly downstream from the effluent of a municipality and paper mill. Sampling depths ranged from 2 to 6 m and current velocities ranged from 5 to 50 cm/s.

Sampling was conducted by divers working directly on the bottom of the river using a Johnson Air-Buoy diving unit. This system consists of a floating air compressor which pumps air through two 10-m long hoses to two divers. In practice, the compressor was tied to a boat and one biologist dived while the other remained in the boat to tend the compressor and watch for floating debris which might become entangled in the air hose. The divers quickly acclimated to working in a current. Water velocities below about 30 cm/s presented little problem. In stronger currents a creeper, described by Gale and Thompson (1974b), was needed for maneuvering on the bottom.

Six replicates of each method were taken at each of the four sites. For one sampling method, commercially available wire baskets (Androck Co., Worcester, Mass.; cylinders 16 cm diameter and 26 cm long) were filled with stones of a uniform size (construction grade 6.35 cm). The artificial substrates were equally spaced on a 3-m long nylon line which was tied to a steel rod and driven into the river bottom. The line was placed so that it was parallel to the main flow of the water, at least 30 m from shore in an area of fast-current conditions and a rubble bottom. The substrates were left in position for approximately 4 wk. Substrates were retrieved by a diver who swam up to a basket from downstream holding a fine (no. 60) mesh nylon collection bag. The basket was then carefully lifted and placed in the collection bag and brought to the surface. The stones were individually cleaned, and washings were concentrated through a no. 30 brass screen (0.6-mm openings) and preserved in 5% formalin.

The second sampling technique used a modification of the Hess bottom sampler (Hess 1941) to obtain quantitative invertebrate samples from a prescribed area of stream bottom ($^1/_{16}$ m^2). The sampler was modified so it could be used at any depth by adding a sleeve to the top to prevent the escape of bottom materials when the top was submerged (Fig. 1). The biologist swam to the bottom with the sampler and pressed it firmly onto the substratum. By kicking vigorously he kept the sampler tight to the river bottom, and there was little or no organism loss. The biologist inserted his arm through the sleeve, completely disturbed the enclosed rubble, and the dislodged organisms and other debris were carried by the current into the detachable collecting bag (40-mesh nylon monofilament cloth with 0.4-mm openings). The collection was then brought to the surface and prepared for later analysis as previously stated.

Results and discussion — The artificial substrates

FIG. 1. Modified Hess sampler.

tended to collect more taxa and many more individuals than did the modified Hess sampler at each site (Table 1). The coefficient of variation between samples at a site for numbers of taxa and individuals was lower using the artificial substrates at the polluted and highly polluted sites but similar at the other two sites. As pollution increased the coefficients of variation of the artificial substrates remained constant for the number of taxa collected but increased fourfold for the number of individuals collected. As pollution increased the coefficients of variation for the Hess sampler increased fourfold or more for the number of individuals and the number of taxa collected. Sampler efficiency apparently decreases as pollution increases but there is a greater loss of efficiency with the Hess sampler.

The coefficients of variation from the nonpolluted sites are low, which may be due to the relatively homogeneous habitat of the deep river. Factors affecting the microdistribution of benthic invertebrates, especially the current velocity, are more uniform at the substratum of a deep river than in a smaller stream.

Another test of the efficiency of the sampling methods is to determine how many samples of each type are necessary to be 95% confident that the mean number of taxa or individuals is within a certain percentage (usually 20% in benthic studies) of their true values. The method of Elliott (1971), developed especially for benthic invertebrates, was used and the results are given in the last column of Table 1. Both sampling methods were so efficient that only one sample of either type was necessary to be 95% confident that the mean number of taxa was within 20% of the true value in all cases except two. To obtain the same precision for the mean number of organisms, four or fewer samples were necessary from six of the eight trials.

The efficiencies noted so far refer only to how well the sampler collected a particular segment of the actual benthic community and say nothing about its selectivity. To examine sampling bias, the relative proportions of each invertebrate group collected by each method were compared at the sites (Table 2). The percentages at the two polluted sites are presented with and without

TABLE 1. Mean number of taxa and mean number of individuals (in parentheses) from six replicate samples collected with each type sampler. C.V. = coefficient of variation.

	$\bar{x} \pm SD$	C.V.	No. samples needed to be within 20% of true mean
Pristine			
Artificial substrate	21.8±3.7 (161.1±18.5)	16.9 (11.5)	1 (1)
Hess	15.3±1.9 (74.8±10.4)	12.4 (13.9)	1 (1)
Enriched			
Artificial substrate	20.3±2.8 (510.0±147.6)	13.8 (28.9)	1 (2)
Hess	21.5±3.0 (127.3±41.1)	14.0 (32.3)	1 (3)
Polluted			
Artificial substrate	21.0±3.4 (1053.0±423.0)	16.2 (40.1)	1 (4)
Hess	13.3±3.0 (101.5±61.9)	22.6 (60.9)	2 (9)
Highly polluted			
Artificial substrate	16.3±2.3 (2033.0±773.0)	14.1 (38.0)	1 (4)
Hess	8.1±4.0 (31.3±18.5)	49.4 (59.1)	6 (9)

oligochaetes, whose abundance often masked the samplers' ability to collect other taxa.

The similarities of percentage catch between the two samplers at any one site are more apparent than the differences. Wide discrepancies could usually be attributed to how well the artificial substrate represented a preferred habitat for a particular species. For example, with an increase in pollution the artificial substrates become positively biased for tubificid worms (Table 2). More fine organic matter accumulated in the abundant interstices of the artificial substrate than on the natural substratum and therefore optimized the preferred habitat for this group. At the enriched site the stone interstices did not fill with organic matter and therefore provided an ideal net-attachment site for the abundant hydropsychid caddisflies. The artificial substrates could also be negatively biased as shown by the disproportionate percentage of riffle beetles (Coleoptera: Elmidae) captured by the Hess sampler at the pristine site. These organisms prefer a habitat of wood and other debris which is not usually associated with the rock baskets.

An average of 60% of the taxa was collected by both samplers. Twelve percent of the taxa were collected only by the Hess sampler and 25% only by the artificial substrates. These figures may be misleading, however, because 75% of those taxa collected only by the Hess sampler and 73% of those collected only by artificial substrates were represented by a mean of less than one organism per sample. There were only three taxa that were found in greater abundance than five per sample with one sampler (all artificial substrates) while not being collected at all with the other. The artificial substrates were more efficient in detecting rare taxa, but both samplers were efficient at collecting more common forms.

Loss on retrieval—To determine the possible losses of organisms if artificial substrates were retrieved without precautions, as they often are when attached to buoys or piers, the invertebrates that dropped into the outer collection bag were kept separate from those remaining in the artificial substrates during a series of collections at one of the sites. Mollusca and Crustacea, with little or no means of clinging, showed losses of 92 and 68%, respectively. Diptera, mainly Chironomidae, had a 29% loss. Even those invertebrates with means of holding on showed losses: Ephemeroptera 30%, Trichoptera 26%, and Plecoptera 8%.

The invertebrate communities of large rivers contain a wide variety of lotic forms but the standing crop is

TABLE 2. Percent of the major groups in collections made by each method at each site. Numbers in parentheses are percentages with oligochaetes omitted. H = Hess sampler, AS = artificial substrate.

	Pristine		Enriched		Polluted		Highly polluted	
	H	AS	H	AS	H	AS	H	AS
Trichoptera	7	7	8	23	4 (4)	2 (5)	12 (14)	<1 (16)
Plecoptera	4	9	2	1	0 (0)	<1 (<1)	0 (0)	0 (0)
Ephemeroptera	27	31	26	17	6 (7)	2 (6)	3 (3)	<1 (2)
Megaloptera	2	0	2	1	1 (1)	<1 (2)	3 (4)	<1 (<1)
Odonata	1	1	1	<1	0 (0)	<1 (<1)	0 (0)	<1 (<1)
Coleoptera	24	6	2	<1	1 (1)	<1 (<1)	0 (0)	0 (0)
Diptera	30	36	52	57	55 (64)	19 (55)	30 (36)	4 (43)
Oligochaeta	4	0	2	0	13	65	15	92
Hirudinea	0	0	3	<1	11 (13)	5 (13)	33 (39)	3 (36)
Crustacea	0	0	1	<1	0 (0)	<1 (<1)	3 (4)	<1 (<1)
Gastropoda	1	8	0	0	9 (10)	6 (17)	0 (0)	0 (0)

not as great as would be found in a shallow rubble-bottom stream. Placing rock-filled baskets into this habitat produced a more favorable substratum condition and many species became concentrated. The artificial substrates therefore collected a wider variety and greater number of organisms with more precision than the modified Hess sampler.

Although the Hess sampler may be biased for some forms, e.g. deep burrowing or strongly attached, what it collects must certainly more closely represent actual community structure than the colonization of an alien habitat as represented by the rock-filled basket. Therefore, the Hess sampler is recommended where information approximating standing crop is required. Unfortunately, as bottom-rubble size increases beyond large grapefruit size, or the current velocity drops below approximately 8 cm/s, the sampler becomes inefficient or unusable. The Hess samples have the advantage of being taken on one dive on 1 day, while use of artificial substrates requires two dives, 4 wk apart. Although more Hess samples were needed in many cases to achieve a desired level of precision, separation of invertebrates from detritus took only one third to half as much time for a Hess sample as for a sample from an artificial substrate.

Acknowledgments — Funding for this study was provided by a United States Environmental Protection Agency grant administered through the Maine Department of Environmental Protection. We thank Dr R. W. Hatch, Cooperative Fishery Research Unit, University of Maine at Orono, for reviewing the manuscript.

ANDERSON, J. B., AND W. T. MASON JR. 1968. A comparison of benthic macroinvertebrates collected by dredge and basket sampler. J. Water Pollut. Control Fed. 40: 252–259.

BENFIELD, E. F., A. C. HENDRICKS, AND J. CAIRNS JR. 1974. Proficiencies of two artificial substrates in collecting stream macroinvertebrates. Hydrobiologia 45: 431–440.

CROSSMAN, J. S., AND J. CAIRNS JR. 1974. A comparative study between two different artificial substrate samplers and regular sampling techniques. Hydrobiologia 44: 517–522.

ELLIOTT, J. M. 1971. Some methods for the statistical analysis of samples of benthic invertebrates. Freshwater Biol. Assoc. UK Sci. Publ. 25: 144 p.

GALE, W. F., AND J. D. THOMPSON. 1974a. Placement and retrieval of artificial substrate samplers by SCUBA. Prog. Fish Cult. 36: 231–233.

1974b. Aids to benthic sampling by SCUBA divers in rivers. Limnol. Oceanogr. 19: 1004–1007.

HESS, A. D. 1941. New limnological sampling equipment. Limnol. Soc. Am. Spec. Publ. 6: 1–5.

MASON JR., W. T., J. B. ANDERSON, R. D. KREIS, AND W. C. JOHNSON. 1970. Artificial substrate sampling, macroinvertebrates in a polluted reach of the Klamath River, Oregon. J. Water Pollut. Control Fed. 42: R315–R328.

RABENI, C. F. 1977. Benthic macroinvertebrate communities of the Penobscot River, Maine, with special reference to their role as water quality indicators. Ph.D. Thesis. Univ. Maine, Orono, Maine. 169 p.

WEBER, C. I. 1973. Biological field and laboratory methods for measuring the quality of surface waters and effluents. Environmental monitoring series. EPA-670/4-73-001. Environ. Prot. Agency, Cincinnati. 146 p.

Outplant Method for Phenological Studies of *Chondrus crispus* in Mechanically Harvested Beds

L. A. HANIC

Biology Department, University of Prince Edward Island, Charlottetown, P.E.I.

AND J. D. PRINGLE

Department of Fisheries and the Environment, Fisheries and Marine Service, Resource Branch, Halifax, N.S. B3J 2S7

HANIC, L. A., AND J. D. PRINGLE. 1978. Outplant method for phenological studies of *Chondrus crispus* in mechanically harvested beds. J. Fish. Res. Board Can. 35: 336–338.

A method is described employing a primary pottery unit for seeding and growing *Chondrus crispus* Stackhouse and a secondary concrete platform for support and protection. The combined units facilitate long-term studies where frequent removal of plants for observation is required and where field conditions are adverse.

Key words: Chondrus crispus, Irish moss, seeding, outplanting method

Printed in Canada (J4900)
Imprimé au Canada (J4900)

HANIC, L. A., AND J. D. PRINGLE. 1978. Outplant method for phenological studies of *Chondrus crispus* in mechanically harvested beds. J. Fish. Res. Board Can. 35: 336–338.

Nous décrivons une méthode selon laquelle une unité de base en poterie est utilisée pour l'ensemencement et l'élevage de *Chondrus crispus* Stackhouse et une plate-forme secondaire en ciment pour le support et la protection. Ces unités combinées facilitent les études à long terme au cours desquelles il faut effectuer de fréquents prélèvements de plantes pour observation et là où les conditions sur le terrain sont difficiles.

Received June 28, 1977
Accepted December 8, 1977

Reçu le 28 juin 1977
Accepté le 8 décembre 1977

THERE is a paucity of information on the growth, in situ, of benthic marine algae, particularly from spore to mature plant. These data are lacking for the commercially important alga *Chondrus crispus* Stackhouse but are required for resource management. A prime requirement for obtaining phenological data for resource management is that they should come from areas under exploitation. However, this is difficult in Prince Edward Island *Chondrus* beds where harvesting methods include heavy steel rakes dragged through the beds by boat. In addition, frequent storms and winter ice combined with shallow sloping shores increase the difficulties for long-term observations or experiments. Taylor (1972) attempted long-term growth observations within commercial beds by embedding *Chondrus* into cement blocks; however, these were removed by drag rakers. This note describes a method currently being used successfully by us. The method employs two units: a primary pottery unit on which *Chondrus* is seeded and grown and a secondary concrete unit to which the pottery units are attached.

Materials and methods — Pottery and concrete platforms — The primary pottery units were constructed of Nova Scotia red clay using a mold process. The design includes a low sturdy profile, with depressions for spore inoculation, coarse texturing to thwart browzing *Littorina*, and a hole for a screw attachment (Fig. 1A, B). For details on preparation, see Hanic and Pringle (1978). The pottery units are seeded with spores in the laboratory and following germination are out-planted into the field on a secondary platform.

The secondary unit consists of a concrete slab 120 × 60 × 15 cm (length × width × depth) having four longitudinal grooves for placement and protection of the seeded pottery units and tapered edges to reduce snagging. The concrete slab was made in a wooden form to the bottom of which four longitudinal wooden slats, 9 × 2 cm (width × depth), with tapered edges were attached. Twenty plastic screw anchors were affixed to each wooden slat with screws, facing into the mold. Steel reinforcing rods (13 mm diam), two running lengthwise and four crosswise, were positioned in middepth with wire. Two to four plastic pipes (2.5 cm diam) were incorporated in the mold to provide holes for anchorage. The form was filled with concrete (sand and cement only, 3:1 ratio). After 24 h the screws were removed, leaving the plastic screw anchors embedded in the concrete (Fig. 1C). Another 4–6 days were allowed for curing before placement in the sea.

The concrete blocks were secured to the ocean bottom by bolts (1.3 mm diam × 30 cm long) fastened at the base with cinch anchors (Fig. 1C, D). Holes of 1.5 mm diam were drilled into the ocean bottom with a specially built underwater hydraulic drilling apparatus, consisting of a reversible drill, Model No. 6H-67 (Ackley Manufacturing Co. Ltd. Portland, Oreg.), 25 metres of hydraulic hose (1.27 mm inside diam), a 16 hp (11.9 kW) air-cooled gasoline Briggs and Stratton engine (Milwaukee, Wis.), an oil reservoir (43 × 43 × 12.7 cm), and a hydraulic pump (Model #9, Gresen Co., Minneapolis, Minn.) mounted on a portable steel frame. This unit is sufficiently compact that it can be operated in a 6-m fiberglass boat (Boston Whaler Inc., Boston, Mass.), leaving room for three SCUBA divers and gear and two concrete platforms.

Seeding — The primary pottery units were autoclaved 3 times in three changes of seawater for conditioning purposes (Hanic and Pringle 1978a). Large plants with abundant, mature sori were cleaned of epiphytes, dipped for 1–2 s in 100% ethyl alcohol, then rinsed and cut up into sections, and placed into pasteurized seawater (enriched with 72.2 mg KNO_3, 8.8 mg KH_2PO_4, and 0.5 mg Fe ethylenediaminetetraacetic acid per litre) in Petri plates and allowed to discharge under low light of 500–1,000 lx, supplied by cool white fluorescent tubes in a daily 16-h photoperiod. Spores were pipetted into the depressions of previously wetted damp pottery units and allowed to sit for a few minutes prior to placing in trays or bottles of fresh culture media. An alternative method was to use covered plastic trays 70 × 30 cm, the bottoms of which were covered with pottery units. The spores were then pipetted over the surface, providing more uniform seeding. Diatoms, the most frequent contaminant, were inhibited by use of germanium dioxide. Germling development varied with the stock; in absence of contaminating algae and use of frequent nutrient changes, germlings up to 2 mm long were obtained in 2 mo. The pottery units with developing plants were transported to the study site and secured with brass screws (Fig. 1C) to the concrete platforms via the embedded plastic wall mounts.

Relocation — Because visibility is frequently poor (<3 m) in coastal Prince Edward Island waters and because *Chondrus* beds are located comparatively long distances offshore (up to 1500 m), relocation using surveyor transects only (our original method) proved too costly in time and money. This method is being augmented by an electronic pinger–receiver system for rapid final location. The pinger is placed into a hole drilled into the concrete platform itself for protection. (Details on the construction of the pinger–receiver system and drilling unit are available from J. D. Pringle.)

Evaluation of method — The primary seeded pottery

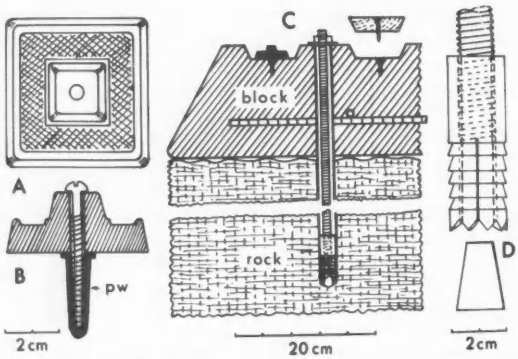

FIG. 1. A and B, Pottery unit in surface view (A) and longitudinal section (B) showing rough textured depression for seeding (crosshatching) and mode of attachment via screw and plastic wall mount (pw). C, Longitudinal section of one half of concrete platform showing longitudinal grooves into which the pottery unit (solid black) is attached, method of attachment via bolt and cinch anchor, two reinforcing rods, slat in cross section and screw shown removed from groove leaving plastic wall mount embedded in the concrete. D, Enlargement of cinch anchor and spreader.

units and secondary concrete blocks have been placed in four localities at different depths off Prince Edward Island: Egmont Bay, Morrissey's Cove, Miminegash, and West Pubnico, N.S. These have now survived up to 3 yr, during which the worst gale in 100 yr (February 2, 1975) struck the Maritime Provinces, causing extensive damage to harbor facilities, boats, and submerged fishing gear. The units (both pottery and concrete) stood up well, despite some being located only 20 cm below mean low water. Ice scouring during the winter of 1975–76 split one block of seven placed off Miminegash. However, the block held together and remained in place. Some pottery units were dislodged but were found nearby and undamaged. Drag-rake scars were found on one concrete block in Egmont Bay, but only 1 pottery unit out of 40 on this block was lost. In the Miminegash area, during early summer of 1976, when harvesting was most intensive (100 harvesters dragging at the season's peak), a number of blocks received scars and three were dislodged. These were of the original design with square edges. Tapering the block edges (Fig. 1C) has reduced this problem.

The primary units accept the *Chondrus* spores well and provide firm anchorage. Results on growth rates and morphological variability have been obtained over a 3-yr period (Hanic and Pringle unpublished data). On the basis of these results, it can be estimated with confidence that the present units will yield information for another 3 yr and probably longer, a sufficient time to grow *Chondrus* through its complete life cycle in the sea.

Acknowledgments — We thank J. Jenkins for assistance in early outplant experiments; D. Smith, J. Carter, D. Roddick, and B. Semple for field assistance. Financial support was provided (Hanic) by the National Research Council, Grant No. A9637, the University of Prince Edward Island Senate Research Fund, and the P.E.I. Department of Fisheries.

HANIC, L. A., AND J. D. PRINGLE. 1978. Pottery, a substrate for algal culture. Br. Phycol. J. 13. (In press)

TAYLOR, A. R. A. 1972. Growth studies of *Chondrus crispus* in Prince Eward Island, p. 29–36. *In* Proc. on the Atlantic Seaweed Industry, 1971. Ind. Dev. Branch, Fish. Serv., Ottawa, 149 p.

Survey of Trace Metal Contents of Suspended Matter in the St. Lawrence Estuary and Saguenay Fjord

D. COSSA[1]

Section d'Océanographie de l'Université du Québec à Rimouski (SOUQAR), Rimouski, Qué.

AND S. A. POULET

Institut National de la Recherche Scientifique (INRS-Océanologie), Université de Québec, Rimouski, Qué. G5L 3A1

COSSA, D., AND S. A. POULET. 1978. Survey of trace metal contents of suspended matter in the St. Lawrence estuary and Saguenay fjord. J. Fish. Res. Board Can. 35: 338–345.

Trace metal contents (Mn, Zn, Pb, and Cd) of suspended particulate matter were measured in the upper St. Lawrence estuary and Saguenay fjord. In the estuary, elution of

[1]Present address: INRS-Océanologie, 310 Ave. des Ursulines, Rimouski, Qué. G5L 3A1.

Printed in Canada (J4763)
Imprimé au Canada (J4763)

the trace metal fraction adsorbed on particles seems to be mostly responsible for the significant differences in concentrations observed at the freshwater–saltwater boundary. In the Saguenay fjord, particles from deep waters are enriched with trace metals, especially Mn, compared with those from surface waters. This enrichment is probably due to Mn oxidation and simultaneous scavenging of the other trace elements. High Pb and Cd levels in particles of surface waters of the fjord seem to depend mostly on their high affinity for the rich organic matter.

Key words: trace elements, suspended matter, estuaries, manganese, zinc, lead, cadmium

COSSA, D., AND S. A. POULET. 1978. Survey of trace metal contents of suspended matter in the St. Lawrence estuary and Saguenay fjord. J. Fish. Res. Board Can. 35: 338–345.

Les contenus en métaux en traces (Mn, Zn, Pb et Cd) du matériel particulaire en suspension ont été mesurés dans les eaux de l'estuaire moyen du Saint-Laurent et du fjord du Saguenay. Dans l'estuaire moyen on observe des différences significatives entre les concentrations mesurées de part et d'autre de la frontière de l'eau douce et de l'eau salée qui semblent résulter principalement de l'élution de la fraction des métaux en traces adsorbés sur les particules. Dans le fjord du Saguenay, on constate un enrichissement en métaux en traces, tout particulièrement en Mn, dans les particules des eaux profondes par rapport à la surface; ceci est probablement dû à la formation d'oxydes de Mn et à la sorption simultanée des autres éléments en traces. Les fortes concentrations de Pb et Cd des particules dans les eaux de surface du fjord dépendent probablement de leur grande affinité pour les particules riches en matière organique présentes.

Received March 23, 1977
Accepted December 13, 1977

Reçu le 23 mars 1977
Accepté le 13 décembre 1977

THE redistribution of trace metals among the solid and dissolved phases in estuaries seems to be one of the most important processes affecting the fate of trace metals in natural waters, but it is poorly understood. Duinker et al. (1974) have observed a decrease of metal content of suspended particles between the upper and lower Rhine estuary. Evans and Cutshall (1973) found a partial desorption of ^{65}Zn and ^{57}Mn for the particulate matter of the Columbia River estuary within low-salinity zones. Similar patterns have been reported for mercury (Bothner and Carpenter 1973) and zinc (Fukaï et al. 1975). Conversely, measurements made by Lowman et al. (1966) have illustrated the mechanism involved in the precipitation of trace metals dissolved in river waters which takes place after mixing with salt water. Recent works (Graham et al. 1976; Duinker and Nolting 1976; Grieve and Fletcher 1977) have indicated for several metals the coexistence of these two processes in the estuarine system.

In St. Lawrence estuary, the quantity of suspended matter transportal is quite low (D'Anglejan 1969, 1970; D'Anglejan and Smith 1973; Sundby 1974). Troude (1975), D'Anglejan and Ingram (1976), and Sundby and Silverberg (1977) have described the particulate matter transport and distribution in the upper estuary with reference to the high turbidity zone. No systematic data are yet published on the trace metal composition of these suspended particles. In the Saguenay fjord, the main tributary of the St. Lawrence estuary, trace metal distribution in sediments (Loring 1975, 1976a, b) and in water, though not for the particulate form, (Yeats and Bewers 1976) are available.

We describe and compare the variation of some trace metals (Mn, Zn, Pb, and Cd) in suspended particulate matter found in the upper St. Lawrence estuary and Saguenay fjord.

Materials and methods — Samples were collected with 12-L Niskin bottles modified as described by Bewers et al. (1974) on 22 stations located in the upper St. Lawrence estuary and Saguenay fjord (Fig. 1). Samples were filtered through Metricel membranes (47 mm diameter, 1.2 μm pore size) under pressure (Sundby 1974) until the filter clogged. Fifty percent of the filtrations were replicated. Volumes of water filtered were measured and membrane filters stocked in Petri dishes and stored at −10°C.

Concentrations and sizes of the particulate matter within the 1–200-μm range were measured on board with a Model TA Coulter counter. A factorial analysis was performed on the particle size distribution to characterize the different water masses in terms of particle-size spectra (Kitchen et al. 1975; Chanut et al. 1977).

Samples for trace metal analysis were freeze-dried in the laboratory and digested with 2 mL of concentrated (70%) nitric acid (Ultrex, Baker) for 2 h at 100°C in Teflon bombs. The acid-soluble fraction of Mn, Zn, Pb, and Cd was analyzed using an atomic absorption spectrophotometer with graphite furnace and background corrector (Perkin Elmer 306, HGA 2000). Calculations for trace metal content of suspended particles were based on the weight of the particles collected on Nuclepore filters (47 mm diameter, 0.4 μm pore size) during the same cruise (B. Sundby, Section d'Océanographie, Université du Québec à Rimouski, personal communication).

Results and discussion — Upper St. Lawrence estuary — Salinity, turbidity, and particle-size distributions are illustrated in Fig. 2 and spatial variations of the trace metal content of particles in Fig. 3. Manganese, zinc, cadmium, and lead have similar distribution patterns. The highest concentrations are located in the upper re-

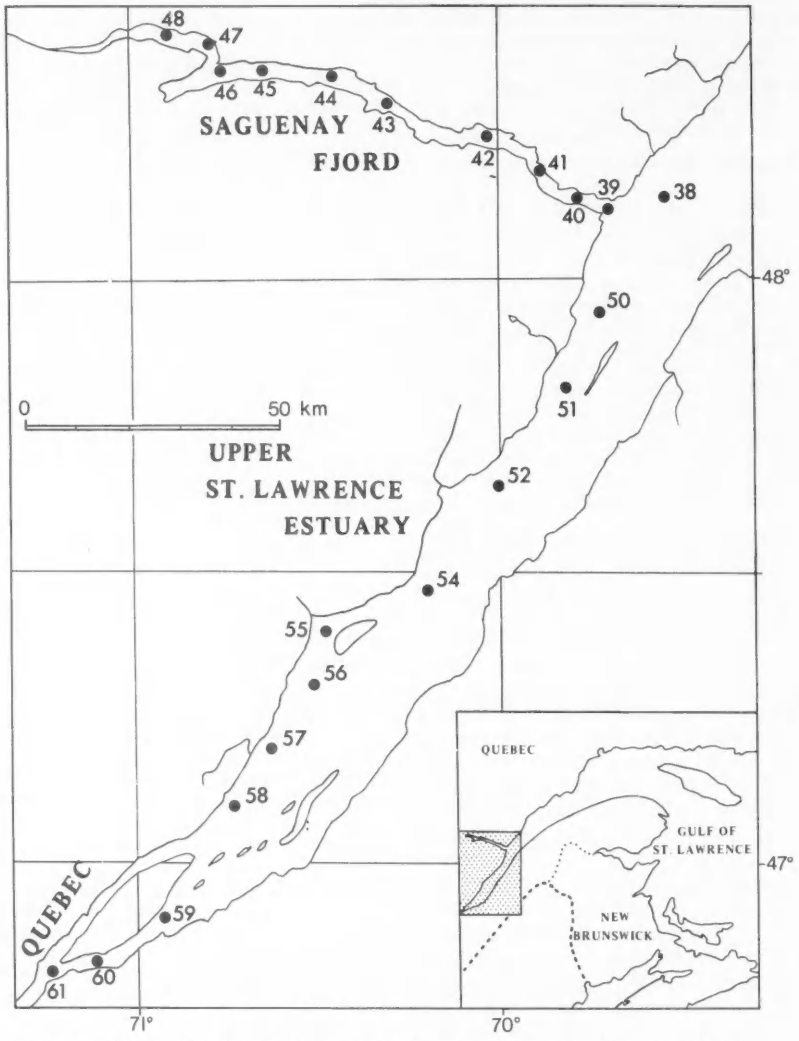

FIG. 1. Station locations in the upper St. Lawrence estuary and Saguenay fjord.

gion of the estuary, whereas the lowest concentrations are in the lower region. Mean concentrations were computed between areas A and B (Table 1), that is, above and below the limit of salt intrusion (between station 59 and 58, Fig. 2c). The average concentrations for each metal were significantly different ($P \leq 0.05$) for the two areas. The *t*-tests also show the same level of significance when the calculations in areas A and B take into account only the samples from zone 1 (Fig. 2c). Consequently these trace metal concentration differences do not reflect variations related to the size of particles.

In the upper St. Lawrence estuary, D'Anglejan and Smith (1973) have reported the importance of the min-

TABLE 1. Comparison of means of the trace metal concentrations ($\mu g \cdot g^{-1}$) in particles from the upper St. Lawrence estuary. Area A corresponds to stations 59–61, area B to stations 50–58. $^*P \leq 0.05$.

	Area A		Area B		
	Mean ± SD	(*n*)	Mean ± SD	(*n*)	*t*-test
Mn	1809 ± 273	(11)	766 ± 108	(19)	*
Zn	403 ± 89	(11)	240 ± 79	(19)	*
Pb	96 ± 26	(11)	48 ± 12	(19)	*
Cd	1.8 ± 0.5	(11)	0.9 ± 0.7	(19)	*

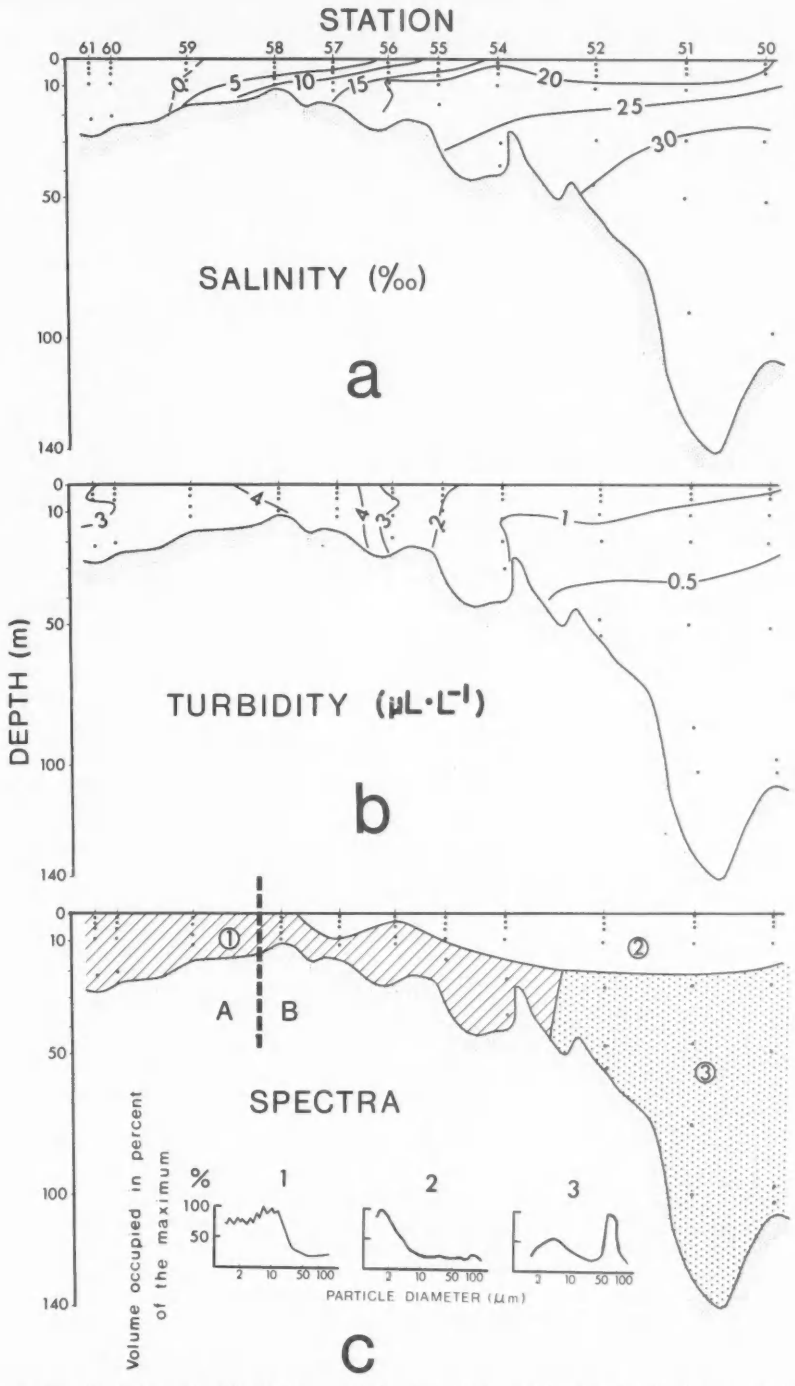

FIG. 2. Variations of salinity (a), turbidity (b), and particle size (c) in the upper St. Lawrence estuary. In Fig. 2c each zone corresponds to a particle-size spectrum. Line A/B locates the freshwater–saltwater interface.

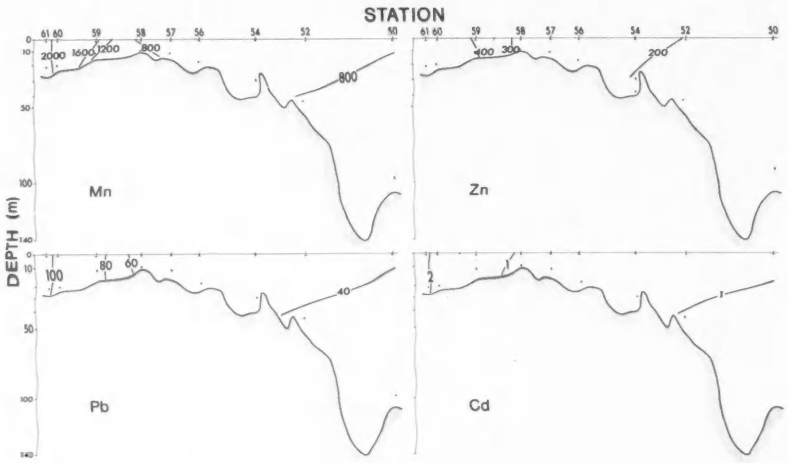

FIG. 3. Variations of the manganese, zinc, cadmium, and lead concentrations ($\mu g \cdot g^{-1}$) in particles from the upper St. Lawrence estuary.

eral fraction which can account for up to 90% of the total suspended matter. According to these authors a high proportion of the fine mineral is composed of illite, whose structure is very favorable to ion exchange and adsorptive processes. The decrease in trace metal contents of the nitric-acid-soluble fraction of particles observed at low salinity (~0–5‰) likely results from a variation in the metal ions activity and from a competition for the adsorption sites from cations of seawater.

Saguenay fjord — Within the Saguenay fjord, the differences in salinity, turbidity, and particle-size distributions (Fig. 4) between the upper layer and the water below were evident. Figure 5 illustrates the trace metal content of suspended particles measured at three different depths. Concentrations of manganese, zinc, and cadmium were roughly uniform in the surface layer from the head to the sill of the fjord. In contrast, concentrations were much higher in the water column below the surface, in both the inner and outer basin. Lead concentration was almost constant in the entire fjord. Mean concentrations for each trace metal were significantly different between zones 1 and 2 (Fig. 4c) for manganese and zinc ($P \leq 0.01$) and cadmium ($P \leq 0.05$) (Table 2).

TABLE 2. Comparison of means of the trace metal concentrations ($\mu g \cdot g^{-1}$) in particles from the Saguenay fjord. Zones 1 and 2 are similar to those defined in Fig. 4c. $^{*}P \leq 0.05$, $^{**}P \leq 0.01$.

	Zone 1		Zone 2		
	Mean ± SD	(*n*)	Mean ± SD	(*n*)	*t*-test
Mn	1090 ± 250	(18)	3500 ± 1775	(17)	**
Zn	272 ± 79	(18)	497 ± 173	(16)	**
Pb	134 ± 48	(18)	136 ± 66	(17)	—
Cd	2.2 ± 1.5	(18)	3.9 ± 2.0	(16)	*

In the surface waters of the fjord, enrichment of Pb and Cd in particles is evident when concentrations are compared with the measurements made in the estuary (Tables 1 and 2). Our results are consistent with the high lead concentrations in particles already measured for surface sediments by Loring (1976a), who assumes that the lead may have come from sources at the head of the Saguenay fjord. Discharge of high contents of particulate organic matter revealed by the composition of recent surface sediments near the head of the fjord (Loring and Nota 1973; Pocklington 1975) should promote the formation of Cd and Pb rich particles because of the high affinity of these metals for the organic matter.

In the deep waters of the fjord the metal enrichment of particles compared with surface waters is maximum for Mn. This high Mn content of particles (Table 2, zone 2) is probably due to an authigenic formation of manganese oxides which may result from the precipitation of dissolved manganese released from the bottom sediments by diagenesis (Price and Calvert 1973). This is enhanced by a high content of dissolved oxygen measured by Taylor (1975) in the waters of the fjord. The good adsorption matrix offered by manganese oxides (Krauskopf 1956) could explain that the particles are simultaneously enriched with other trace metals.

In the fjord, it has been shown that the waters below the halocline (zone 2) originate from surface and intermediate waters of the lower estuary (Drainville 1968; Thériault and Lacroix 1975). The higher mean Mn concentration of particles in the inner basin (mean = 4307; SD = 1680 $\mu g \cdot g^{-1}$) compared with that of the outer basin (mean = 1665; SD = 237 $\mu g \cdot g^{-1}$) illustrates

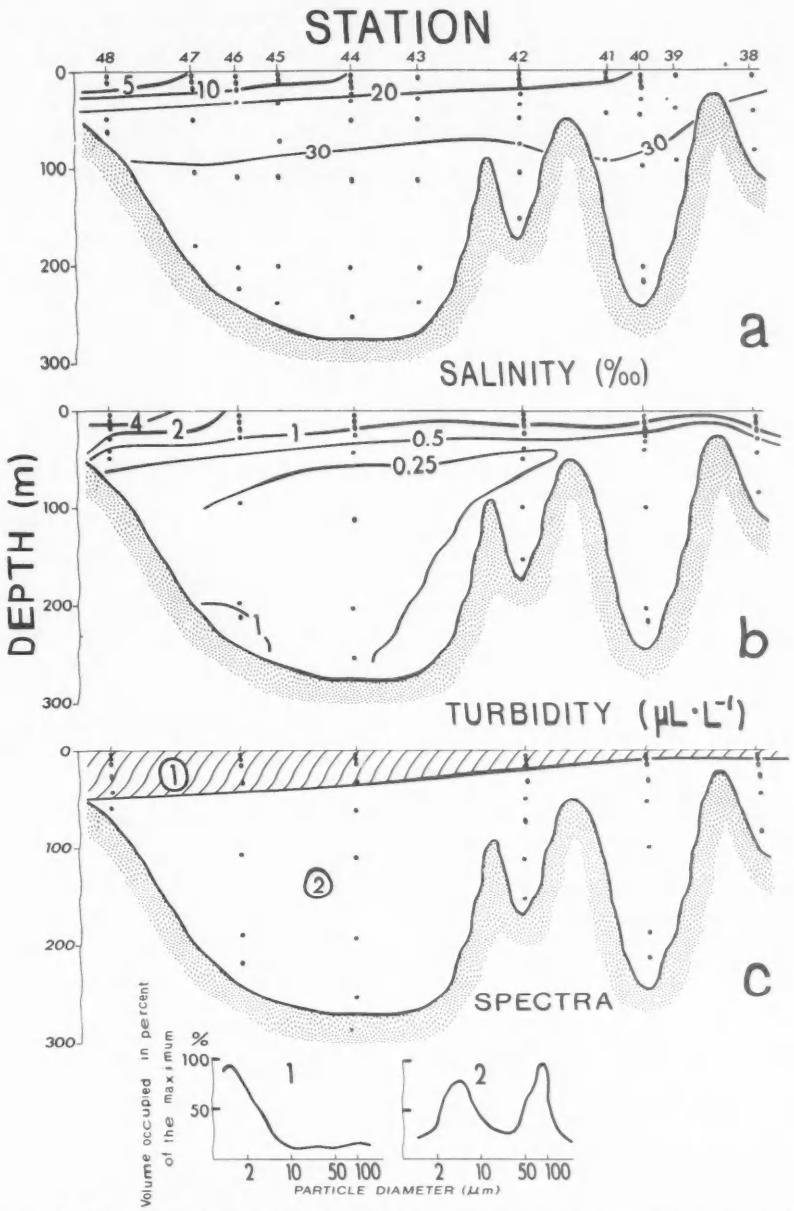

FIG. 4. Variations of the salinity (a), turbidity (b), and particle size (c) in Saguenay fjord. In Fig. 4c each zone corresponds to a particle-size spectrum.

the process of trace metal enrichment of particles within waters temporarily entrapped in the inner basin.

Thus desorption appears to be the source of the major variations of trace metal concentrations observed in the suspended matter at the freshwater–saltwater interface in the upper St. Lawrence estuary. In the Saguenay fjord, higher salinity waters originating from the estuary are probably the site for the formation of hydrous manganese oxides that scavenge other trace metals.

Acknowledgments — We are indebted to Dr B. Sundby for allowing us access to his weight determinations of particles

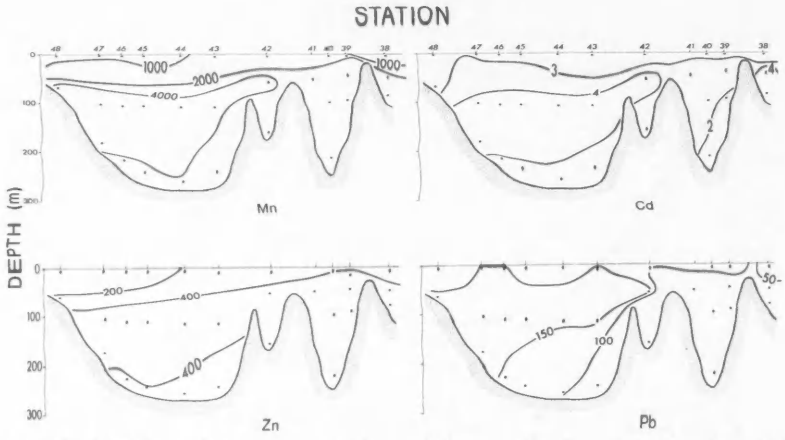

FIG. 5. Variations of the manganese, zinc, cadmium, and lead concentrations ($\mu g \cdot g^{-1}$) in particles from the Saguenay fjord.

and reviewing the manuscript with Dr G. Drapeau. We thank Mr L. Hotton for his technical assistance. We acknowledge the Bedford Institute of Oceanography for shiptime on CSS DAWSON, and for providing the salinity determinations. Thanks are due to Miss E. Goulet for typing. This work was supported by CNRC grants A-9667 and A-4238.

BEWERS, J. M., W. W. HALL, AND I. D. MACAULAY. 1974. A modified Niskin bottle for trace element sample collection. Bedford Inst. Oceanogr. Rep. Ser. BI-R-74-2: 10 p.

BOTHNER, M. H., AND R. CARPENTER. 1973. Sorption and desorption reactions of mercury with suspended matter in Columbia river. IAEA STI-PUB. 313: 73–86.

CHANUT, J. P., S. A. POULET, D. COSSA, AND J. C. MARTY. 1977. Factor analysis of the suspended matter distribution in the St. Lawrence estuarine system. Paper presented at the first world conference on mathematics at the service of man. Barcelona, Spain, July 11–16, 1977.

D'ANGLEJAN, B. F. 1969. Preliminary observations on suspended matter in the Gulf of St. Lawrence. Marit. Sediments 5: 15–18.

1970. Studies in particulate matter in the gulf of St. Lawrence. Mar. Sci. Centre, McGill Univ., Montréal, Qué. Unpubl. Manuscr. Rep. No. 17: 31p.

D'ANGLEJAN, B. F., AND R. G. INGRAM. 1976. Time–depth variations in tidal flux of suspended matter in the St. Lawrence estuary. Estuarine Coastal Mar. Sci. 4: 401–416.

D'ANGLEJAN, B. F., AND E. C. SMITH. 1973. Distribution, transport and composition of suspended matter in the St. Lawrence estuary. Can. J. Earth Sci. 10: 1380–1396.

DRAINVILLE, G. 1968. Le fjord du Saguenay. I. Contribution à l'océanographie. Nat. Can. 95: 809–855.

DUINKER, J. C., G. T. M. VAN ECK, AND R. F. NOLTING. 1974. On the behavior of copper, zinc, iron and manganese and evidence for mobilization processes in the Dutch Wadden sea. Neth. J. Sea Res. 8: 214–239.

DUINKER, J. C., AND R. F. NOLTING. 1976. Distribution model for particulate trace metals in the Rhine Estuary, Southern Bight and Dutch Wadden sea. Neth. J. Sea Res. 10: 71–102.

EVANS, D. W., AND N. H. CUTSHALL. 1973. Effects of ocean water on the soluble–suspended distribution of Columbia river nuclides. IAEA STI-PUB. 313: 125–139.

FUKAÏ, R., C. N. MURRAY, AND L. HUYNK-NGOC. 1975. Variations of the soluble zinc in the Var river and its Estuary. Estuarine Coastal Mar. Sci. 3: 177–189.

GRAHAM, W. F., M. L. BENDER, AND G. P. KLINKHAMMER. 1976. Manganese in Narragansett Bay. Limnol. Oceanogr. 21: 665–673.

GRIEVE, D., AND K. FLETCHER. 1977. Interactions between zinc and suspended sediments in the Fraser river estuary, British Columbia. Estuarine Coastal Mar. Sci. 5: 415–419.

KITCHEN, J. C., D. MENZIES, H. PAK, AND J. R. V. ZANEVELD. 1975. Particle size distributions in a region of coastal upwelling analyzed by characteristic vectors. Limnol. Oceanogr. 20: 775–783.

KRAUSKOPF, K. B. 1956. Factors controlling the concentrations of thirteen rare metals in sea water. Geochim. Cosmochim. Acta 9: 1–32b.

LORING, D. H. 1975. Mercury in the sediments of the gulf of St. Lawrence. Can. J. Earth Sci. 12: 1219–1237.

1976a. The distribution and partition of zinc, copper and lead in the sediments of the Saguenay fjord. Can. J. Earth Sci. 13: 960–971.

1976b. Distribution and partition of cobalt, nickel, chromium and vanadium in the sediments of the Saguenay fjord. Can. J. Earth Sci. 13: 1706–1718.

LORING, D. H., AND D. J. G. NOTA. 1973. Morphology and sediments of Gulf of St. Lawrence. Bull. Fish. Res. Board Can. 182: 147 p.

LOWMAN, F. G., D. K. PHELPS, R. MCCLIN, V. R. DE VEGA, I. O. DE PODOVANI, AND R. J. GARCIA. 1966. Interactions of the environmental and biological factors on the distribution of the trace elements in the marine environment, p. 249–265. *In* Disposal of radioactive wastes into seas, oceans and surface water. Proc. Symp. Vienna 1966. IAEA.

POCKLINGTON, R. 1975. Carbon, hydrogen, nitrogen and

lignin determinations on sediments from the Gulf of St. Lawrence and adjacent waters. Bedford Inst. Oceanogr. Rep. Ser. BI-R-75-6.

PRICE, N. B., AND S. E. CALVERT. 1973. A study of the geochemistry of the suspended particulate matter in coastal waters. Mar. Chem. 1: 169–189.

SUNDBY, B. 1974. Distribution and transport of suspended particulate matter in the gulf of St. Lawrence. Can. J. Earth Sci. 11: 1517–1533.

SUNDBY, B., AND N. SILVERBERG. 1977. Observations in the suspended matter maximum of the St. Lawrence Estuary. Can. Meteor Soc. 11th Annu. congr., Winnipeg, June 1–3, 1977.

TAYLOR, G. B. 1975. Saguenay river sections from twelve cruises 1961–1974. Bedford Inst. Oceanogr. Rep. Ser. BI-D-75-2.

THERRIAULT, J. C., AND G. LACROIX. 1975. Penetration of the deep layer of the Saguenay fjord by surface waters of the St. Lawrence estuary. J. Fish. Res. Board Can. 32: 2373–2377.

TROUDE, J. P. 1975. Salinité des suspensions colloïdales dans l'estuaire moyen du St-Laurent. Thèse de maîtrise. Université Laval, Qué. 164 p.

YEATS, P. A., AND J. M. BEWERS. 1976. Trace metals in the waters of the Saguenay fjord. Can. J. Earth Sci. 13: 1319–1327.

Anesthetic and Handling Stress on Survival and Cortisol Concentration in Yearling Chinook Salmon (*Oncorhynchus tshawytscha*)[1]

RICHARD J. STRANGE[2] AND CARL B. SCHRECK

Oregon Cooperative Fishery Research Unit,[3] Oregon State University, Corvallis, Oreg. 97331, USA

STRANGE, R. J., AND C. B. SCHRECK. 1978. Anesthetic and handling stress on survival and cortisol concentration in yearling chinook salmon (*Oncorhynchus tshawytscha*). J. Fish. Res. Board Can. 35: 345–349.

Brief anesthetization with 50 mg/L buffered MS-222® (ethyl *m*-aminobenzoate methanesulfonate) of yearling chinook salmon (*Oncorhynchus tshawytscha*) during mild handling caused no change in plasma cortisol concentrations compared with levels in non-anesthetized fish. Prolonged exposure (180 min) to a depressing dose of buffered MS-222® (25 mg/L) elevated cortisol more than an immobilizing dose (50 mg/L), while 100 mg/L was lethal within 30 min. Fish anesthetized (50 mg/L MS-222®) during a severe 30-min handling stress had significantly lower mortality than controls to a second handling stress applied when the fish were no longer anesthetized. Anesthetization during the first stressor also prevented the cortisol stress response evident in the control fish. Anesthetic (with or without buffer) administered before initial capture was most effective at increasing survival during a second stressor, while anesthetic supplied after initial capture may have been slightly less effective. A 0.5% NaCl solution supplied after capture was less effective than any anesthetic treatment in increasing future survival, but was better than no treatment. Saline treatment did not attenuate the cortisol stress response. A rapid method of plasma sample preparation for competitive protein binding assay of cortisol was developed.

Key words: chinook salmon, cortisol, stress, anesthetic, cortisol assay, survival

---

[1]Oregon State University Agricultural Experiment Station Technical Paper No. 4716.

[2]Present address: Department of Forestry, Wildlife, and Fisheries, University of Tennessee, Knoxville, Tenn. 37916, USA.

[3]Cooperators are Oregon Department of Fish and Wildlife, Oregon State University, and U.S. Fish and Wildlife Service.

Printed in Canada (J4930)
Imprimé au Canada (J4930)

STRANGE, R. J., AND C. B. SCHRECK. 1978. Anesthetic and handling stress on survival and cortisol concentration in yearling chinook salmon (*Oncorhynchus tshawytscha*). J. Fish. Res. Board Can. 35: 345–349.

Une brève anésthésie à 50 mg/L de MS-222® (éthyl-*m*-aminobenzoate méthanesulphonate) administrée à des saumons chinook (*Oncorhynchus tshawytscha*) de l'année au cours d'une légère manipulation ne cause pas de changement dans les teneurs en cortisol plasmatique comparativement à celles de poissons non anésthésiés. Une exposition prolongée (180 min) à une dose dépressive de MS-222® (25 mg/L) tamponné élève la teneur en cortisol plus qu'une dose immobilisante (50 mg/L), alors que 100 mg/L causent la mort en moins de 30 min. Les poissons anésthésiés (50 mg/L de MS-222®) lors d'un stress causé par une rude manipulation de 30 min subissent des mortalités nettement inférieures à celles des témoins lorsque soumis à une seconde manipulation, alors que les poissons ne sont plus anésthésiés. L'anesthésie lors de la production du premier stress bloque également la réponse du cortisol au stress, évidente chez les témoins. L'anesthésique (avec ou sans tampon) administré avant la capture initiale réussit le mieux à assurer une meilleure survie lors d'un second stress, alors que l'anesthésique administré après la capture initiale peut être légèrement moins efficace. Une solution de NaCl à 0.5% appliquée après la capture est moins efficace que l'anesthésie pour améliorer la survie future mais est supérieure à l'absence de traitement. La saline n'atténue pas la réponse du cortisol au stress. Nous mettons au point une méthode rapide de préparation d'échantillons de plasma pour le dosage du cortisol par liaison compétitive des protéines.

Received July 19, 1977
Accepted December 6, 1977

Reçu le 19 juillet 1977
Accepté le 6 décembre 1977

FISH are subjected to extensive handling during capture, tagging, and transport. Methods decreasing immediate mortality and increasing future survival would benefit culture and management operations. We have investigated the stress imposed by anesthetic and handling and confinement, using resistance to a second stress and plasma cortisol level as a means of quantifying the response. We also evaluated the use of anesthetic and mild saline solution as a means of reducing handling stress.

Anesthetics, primarily MS-222®, are used routinely to immobilize fish during handling procedures. However, the stress that anesthetics place on fish in conjunction with mild handling, the effects of different concentrations of anesthetic, and the influence of anesthetics upon future survival of fish are unknown. Plasma cortisol elevation has been associated with response to a variety of stresses (e.g. Strange et al. 1977; Mazeaud et al. 1977). We compared cortisol concentration in anesthetized and nonanesthetized fish subjected to stresses associated with transfer from one tank to another. Cortisol concentration was also measured in fish exposed continuously to different concentrations of MS-222®. Finally, the value of treatment with buffered and unbuffered anesthetic and 0.5% saline solution during handling was examined in terms of cortisol variation and survival following exposure to a second stress.

Materials and methods — Fish used in the experiments were yearling spring chinook salmon (*Oncorhynchus tshawytscha*) ranging from 9 to 19 cm in fork length from the Rogue River, Oregon. Before experimentation, fish were acclimated under normal photoperiod for at least 1 wk to 60-cm-diameter circular tanks filled to 40 cm with flowing 12°C well water of about neutral pH and hardness of about 100 mg/L as $CaCO_3$. An aqueous stock solution of 50 mg/mL MS-222® was used in the administration of the anesthetic. In the first experiment comparing anesthetization and no anesthetization in the presence of mild handling 0.2 mL 5 M imidazole per 50 mg MS-222®, delivered concurrently, was used as a buffer. This concentration of buffer raised the pH of treated water slightly (0.3 pH unit), and in subsequent experiments 0.05 mL 5 M imidazole/50 mg MS-222® was used; this resulted in a lowering of the pH by 0.1 or 0.2 unit. In contrast, unbuffered MS-222® at 50 mg/L lowered the pH of the water 0.5 pH unit. All plasma samples were obtained as rapidly as possible (within less than 5 min/group) by severing the caudal peduncle and collecting the blood in heparinized capillary tubes; after centrifugation the samples were stored at −15°C.

Competitive protein binding (CPB) assay of cortisol usually employs extraction requiring centrifugation to remove denatured protein (total corticosteroid method of Donaldson and Dye (1975)). We characterized a simplified method in which the ethanol-precipitated protein is left in the assay tube by splitting a series of salmon plasma samples into two aliquots with one aliquot assayed after usual extraction and the other after simply precipitating the protein, thus comparing cortisol values obtained on the same plasma following the two different methods of preparation. Also, different volumes of pooled plasma containing different levels of endogenous cortisol were processed in replicates of 12 by both procedures in order to compare the variability of the two methods over a range of sample conditions.

Plasma samples were extracted by adding 0.5 mL of redistilled ethanol, stirring on a vortex mixer, centrifuging to form a hard pellet (specific centrifuging characteristics are not necessary but we use about 50,000 *g* for 10 min at or below 24°C), and drawing off the ethanol supernatant. After extracting the protein pellet a second time, the combined ethanol fractions were evaporated to dryness. In the simplified procedure, the plasma sample was not extracted but just precipitated with 0.5 mL ethanol, stirred, and evaporated to dryness under air. All samples were assayed by CPB as adapted from Murphy (1967). First, 1.0 mL of 0.5% human male serum (aqueous solution) with cortisol binding sites "saturated" with tritiated cortisol was added to the dried samples in 15 × 85 mm culture tubes. The amount of tritiated cortisol used to saturate a 100 mL of 0.5% serum

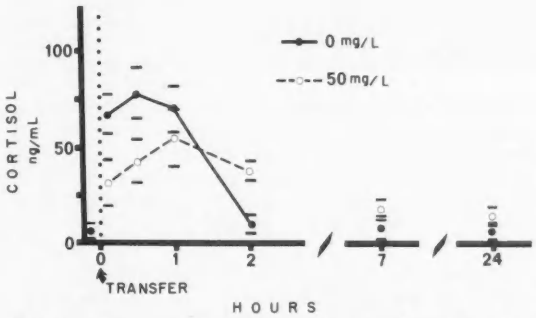

FIG. 1. Plasma cortisol concentration over time of anesthetized (50 mg/L buffered MS-222®) and nonanesthetized yearling chinook salmon subjected to the mild handling stress of transfer to a new tank. Standard errors are indicated around means for six fish.

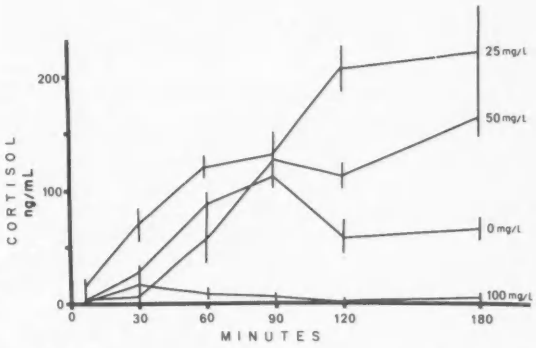

FIG. 2. Plasma cortisol concentration over time of yearling chinook salmon exposed continuously to different levels of buffered MS-222®. Standard errors are indicated around means for six fish. The fish exposed to 100 mg/L were dead by the first sample (30 min).

was 114 ng (29 μCi), although now we use about one third that amount with good results. After allowing the samples to react for 5 min at 45°C (water bath) they were placed in an ice bath, and the unbound corticoids removed by addition of 80 mg Florisil® (activated magnesium silicate, Baker) to each tube, shaking the tube for 30 s on a vortex mixer, and after 3 min removing a 0.5-mL aliquot of Florisil®-free solution for scintillation counting in Insta-Gel® (Packard). Duplicate cortisol standards (0, 0.25, 0.5, 1, 2, 3, 4, 6, 8 ng/tube) were processed along with the unknowns to provide a standard curve, and cortisol concentrations in samples were determined graphically.

Cortisol values obtained by extraction and by simple precipitation on split samples showed a linear relationship ($y = 1.00x + 10.45$, $r^2 = 0.69$, where y equals cortisol measured in extracted samples and x equals cortisol measured in precipitated samples) over a range of 0–200 ng/mL. Replicate determinations ($n = 12$) on two pooled plasma samples (A and B) containing different levels of endogenous cortisol were as follows ($\bar{x} \pm$ SD, nanograms per millilitre): 10-μL subsamples plasma A, extracted 243 $\pm$ 13, precipitated 190 $\pm$ 26; 25-μL subsamples plasma A, extracted 159 $\pm$ 20, precipitated 149 $\pm$ 30; 10-μL subsamples plasma B, extracted 502 $\pm$ 117, precipitated 456 $\pm$ 139. There are no significant differences in the variances in cortisol concentrations between the two methods of sample preparation regardless of endogenous plasma concentration or subsample volume ($P = 0.05$, F-test). We thus felt confident in using the more rapid precipitation technique. We used thin-layer chromatography and radiotracer methods to determine that consistently over 75% of the hormone activity measured by this assay is cortisol. Cortisone contributes to the apparent concentration but is only about 10% as active as an equal amount of cortisol due to its lack of affinity for human serum.

Houston and Woods (1972) determined that blood concentrations of MS-222® reached a maximum of 56 mg/L in trout (*Salvelinus fontinalis*) exposed continuously to 100 mg/L of the anesthetic. We conducted an in vitro test that showed that this level of MS-222® did not affect the CPB assay. In the experiments with MS-222® 10-μL volumes of salmon plasma were assayed.

Experimental design and results — Anesthetic during mild handling — At 0915 on November 11, 1977, one group of about 50 yearling chinook salmon was immobilized by pouring 50 mg/L buffered MS-222® into the covered tank with a minimum of disturbance; six fish were sampled from another group, which was not anesthetized, to establish a prestress plasma cortisol level. Five minutes after anesthetization, the immobilized fish were transferred by dip net to an identical tank supplied with fresh, flowing water, and blood samples were taken from six different fish at 5 min, 30 min, 1 h, 2 h, 7 h, and 24 h after transfer. The group of fish that was not anesthetized was similarly transferred and sampled at the same times.

Anesthetized fish recovered within a few minutes after transfer to fresh water. Unanesthetized fish were considerably more agitated because they tried to avoid capture and struggled in the net, while the anesthetized group showed no visible response to handling. Plasma cortisol concentration increased in anesthetized and nonanesthetized fish after transfer with the anesthetized group having a consistently lower level during the 1st h after transfer but taking longer to return to a pretransfer concentration (Fig. 1). The differences in cortisol concentration were not significant.

Different concentrations of anesthetic — Beginning at 1215 on March 15, 1977, four groups of about 45 yearling chinook salmon each were exposed continuously to either 0, 25, 50, or 100 mg/L (0, 1:40,000, 1:20,000, 1:10,000, respectively) of buffered MS-222®. After introduction of anesthetic, water flow was shut off, the tanks were supplied with aeration, and blood samples were taken at 5, 30, 60, 90, 120, and 180 min.

The group receiving the lowest concentration of MS-222® (25 mg/L) consistently had the highest cortisol concentration (Fig. 2). Most of the 25 mg/L group remained upright but unresponsive throughout the experiment. The fish receiving 50 mg/L had the next

TABLE 1. Plasma cortisol concentration of yearling chinook (*Oncorhynchus tshawytscha*) salmon under different anesthetic and saline treatments before and after a severe 30-min handling stress; controls received no treatment. Percent mortality to an immediately applied second handling stress during which no treatment was given is also presented and the 95% confidence limit (normal approximation).

Date (1977) and treatment	Cortisol (ng/mL, $\bar{x} \pm$ SE) Before capture ($n = 6$)	30–40 min after confinement ($n = 12$)	Mortality ± 95% CI second stressor (%)
April 21			
Control	32±12	260±20	85±14.4
Buffered anesthetic before capture	17±8	13±5	12±13.2
April 29			
Control	38±13	202±25	86±14.0
Unbuffered anesthetic before capture	68±13	85±15	19±15.7
Buffered anesthetic after capture	48±12	74±10	32±18.3
0.5% NaCl after capture	69±9	275±22	62±19.0

highest concentration of cortisol, were completely immobilized within 5 min of receiving the anesthetic, and displayed shallow respiration during the 3-h exposure; two of eight remaining fish in this group failed to recover after return to fresh water. The fish receiving no anesthetic appeared somewhat alarmed by the periodic sampling and the absence of water flow and displayed a moderate increase in cortisol concentration; however, there was no overlap of 95% confidence intervals between the 0 mg/L and the 25 mg/L or 50 mg/L groups at the last sampling time (180 min). The fish receiving 100 mg/L exhibited no respiration and did not recover after return to fresh water at the first sampling period (30 min), although they bled freely and some heart beat was noted for the entire 3-h experimental period. No cortisol elevation was evident.

Anesthetization and saline on future survival — The effect of anesthetization and saline treatment on yearling chinook salmon subjected to handling stress was evaluated in terms of plasma cortisol concentration and the ability to survive a second stress. The first handling stress consisted of dip netting groups of about 45 fish into a small net (30 × 10 cm immersed to 15 cm) suspended in their tank and keeping them confined for 30 min; during this time the water was shut off and aeration supplied. Fish received one of four treatments during this 30 min when the water was shut off: immobilization with buffered and unbuffered MS-222® (50 mg/L) prior to confinement, buffered MS-222® (same dosage) immediately after confinement (chasing and catching the fish as rapidly as possible in the dip net), and 0.5% NaCl supplied after confinement. Fish receiving no treatment except capture and confinement in a net served as controls. Plasma samples were taken before confinement (6 fish per treatment) and after the first (30 min) stress (12 fish per treatment). The second stress consisted of transferring the nets of fish to fresh, flowing water in adjacent tanks and keeping the salmon confined until half the controls (no anesthetic or saline supplied during first stress) were dead. The remaining fish in all treatments were liberated into the tank and posthandling mortality noted. The treatment with buffered anesthetic before capture and a control were conducted on one day and the rest of the treatments and a control were conducted on another day.

The controls had the highest mortality when subjected to the second handling stress and had a dramatic increase in cortisol concentration during the first (30 min) stress (Table 1). Saline solution supplied only during the first stress appeared, but not significantly, to reduce mortality to the second stress, but did not reduce the extent of cortisol elevation during the first stressor. Anesthetic supplied before and during the first stress significantly reduced mortality to the second stress when the fish were no longer in the anesthetic; also, anesthetic significantly suppressed the cortisol elevation during the first stress. Buffered and unbuffered anesthetics supplied before capture reduced mortality the most, while buffered anesthetic supplied after initial netting was the anesthetic treatment that reduced mortality the least, although it was still substantially better than saline or no treatment.

Discussion — Brief anesthetization during mild handling resulted in plasma cortisol concentrations comparable to those in unanesthetized fish (Fig. 1). Fish exposed continuously to depressing levels of anesthetic had high levels of cortisol; these concentrations are ones normally associated with stress. It took more than 1 h for cortisol in the narcotized fish to reach stress levels. Wedemeyer (1970) also found no early (12 min) cortisol response in a salmonid (*Salmo gairdneri*) to an immobilizing dose of MS-222®. The 0 ng/mL group's response does not act strictly as a control, because the activities that elevated cortisol slightly in this group would not have affected the unresponsive, anesthetized individuals. There was no change in cortisol levels due

to death or within 3 h thereafter in fish exposed to 100 mg/L MS-222®. Fuller et al. (1974) noted a decline in plasma cortisol concentration after death in a salmonid (*Coregonus laveretus*).

Anesthetization during severe handling spares the full cortisol stress response experienced by the nonanesthetized fish (Table 1). Corroborating this, Houston et al. (1971) found less hyperglycemia, a secondary stress response probably dependent on cortisol, in anesthetized trout (*Salvelinus fontinalis*) than in nonanesthetized trout handled in the same manner. In our experiments, the anesthetized groups had substantially less mortality to a second stress than control groups, indicating that the initial minutes of shock at the onset of handling are particularly damaging to the organism in terms of future survival and that stress can be attenuated by anesthetics. Supplying buffered anesthetic after initial capture reduced mortality to the second stress the least among the anesthetic treatments; moreover, some very early (<1 h) deaths occurred during the second stress which did not occur in any other group. Apparently anesthetic supplied after the onset of handling places an additional burden on the animals initially, although over the long term this treatment reduced mortality more than saline or no treatment. Saline solution supplied during the first stress appeared to reduce mortality to the second stress without moderating the full cortisol stress response. Perhaps saline has the indirect therapeutic value of reducing osmoregulatory demands (see Wedemeyer 1972) without reducing the stress of handling itself, as anesthetic apparently does. J. R. McComas and C. W. Long (unpublished data) found mild saline reduced mortality substantially when the entire handling stress took place in salted water. The less dramatic reduction in mortality attributable to saline in our experiment was probably because salt was not supplied during the second, lethal stress. Saline may be valuable primarily in reducing the initial mortality of handling, while anesthetic appears to actually spare stress and thus increase chances for future survival.

The results of this study have potential for management application. The 50 mg/L dose of MS-222® immobilizes fish as rapidly as the quickly lethal 100 mg/L dose and is less stressful in terms of the cortisol stress response than 25 mg/L, which merely depresses fish. However, even at 50 mg/L, anesthetization becomes increasingly stressful after 1 h. Anesthetization (50 mg/L, MS-222®) increases the potential for future survival in fish subjected to rigorous handling through attenuation of stress by reduction of initial shock. Supplying anesthetic before handling yields the best results but is probably not often feasible; supplying anesthetic after netting results in better future survival than 0.5% salt solution or no treatment. We evaluated the various treatments only in terms of survival to an immediately applied second handling stress. Changes in normal behavior after anesthetization (Goddard et al. 1974) or potential effects of such things as disease resistance might serve to qualify these statements.

Our experiments also provide a firm link between the appearance of the cortisol stress response and reduced fitness in terms of increased mortality to a second stress, strengthening the potential for use of plasma cortisol concentration alone, as an indicator of sublethal stress of certain kinds.

Donaldson, E. M., and H. M. Dye. 1975. Corticosteroid concentrations in sockeye salmon (*Oncorhynchus nerka*) exposed to low concentrations of copper. J. Fish. Res. Board Can. 32: 533–539.

Fuller, J. D., D. B. C. Scott, and R. Fraser. 1974. Effects of catching techniques, captivity, and reproductive cycle on plasma cortisol concentration in the powan (*Coregonus laveretus*) a freshwater teleost from Loch Lomond. J. Endocrinol. 63: 24 p.

Goddard, C. I., J. W. Lilley, and J. S. Tait. 1974. Effects of M.S. 222 anesthetization on temperature selection in lake trout, *Salvelinus namaycush*. J. Fish. Res. Board Can. 31: 100–103.

Houston, A. H., J. A. Madden, R. J. Woods, and H. M. Miles. 1971. Some physiological effects of handling and tricaine methanesulfonate anesthetization upon brook trout, *Salvelinus fontinalis*. J. Fish. Res. Board Can. 28: 625–633.

Houston, A. H., and R. J. Woods. 1972. Blood concentrations of tricaine methanesulphonate in brook trout, *Salvelinus fontinalis*, during anesthetization, bronchial irrigation, and recovery. J. Fish. Res. Board Can. 29: 1344–1456.

Mazeaud, M. M., F. Mazeaud, and E. M. Donaldson. 1977. Stress resulting from handling in fish: primary and secondary effects. Trans. Am. Fish. Soc. 106: 201–212.

Murphy, B. E. P. 1967. Some studies of the protein binding of steroids and their application to the routine micro and ultramicro measurement of various steroids in body fluids by competitive protein-binding radioassay. J. Clin. Endocrinol. Metab. 27: 973–990.

Strange, R. J., C. B. Schreck, and J. T. Golden. 1977. Corticoid stress responses to handling and temperature in salmonids. Trans. Am. Fish. Soc. 106: 213–218.

Wedemeyer, G. 1970. Stress of anesthesia with M.S. 222 and benzocaine in rainbow trout (*Salmo gairdneri*). J. Fish. Res. Board Can. 27: 909–914.

1972. Some physiological consequences of handling stress in juvenile coho salmon (*Oncorhynchus kisutch*) and steelhead trout (*Salmo gairdneri*). J. Fish. Res. Board Can. 29: 1780–1783.

Facing the Long Term: An Inquiry into Opportunities to Improve the Climate for Research with Reference to Limnology in Canada[1]

J. R. VALLENTYNE[2]

Department of Fisheries and the Environment, Fisheries and Marine Service, Freshwater Institute, Winnipeg, Man. R3T 2N6

Contents

351 ABSTRACT
351 RÉSUMÉ
352 INTRODUCTION
353 BACKGROUND
356 THE CLIMATE FOR RESEARCH
361 OPPORTUNITIES FOR CHANGE
365 GENERAL DISCUSSION
367 ACKNOWLEDGMENTS
367 REFERENCES
368 APPENDIX

[1]This paper is based on a report on freshwater science in Canada prepared by the author for the Ocean and Aquatic Sciences sector of the Fisheries and Marine Service, Department of Fisheries and the Environment. The views expressed here are those of the author and not necessarily those of the Fisheries and Marine Service or the Department of Fisheries and the Environment.

[2]*Present address: Canada Centre for Inland Waters, P.O. Box 5050, Burlington, Ont. L7R 4A6.*

Printed in Canada (J4911)
Imprimé au Canada (J4911)

Abstract

VALLENTYNE, J. R. 1978. Facing the long term: an inquiry into opportunities to improve the climate for research with reference to limnology in Canada. J. Fish. Res. Board Can. 35: 350–369.

Deterioration of the climate for research was the main concern expressed in individual interviews with 125 freshwater scientists. The principal problem cited in the Department of Fisheries and the Environment (DFE) was disruptions to the continuity and time frame essential to research; in universities, declining support for "basic" research; and in both, a perceived lack of attention on the part of governments and the public to measures for the resolution of problems in the long term. These perceptions are analyzed in terms of changing attitudes to environment, research, and science policy from 1957 to 1976. Specific suggestions to improve the climate for research in DFE were: implementation of a policy on research; 3–5 year continuity in funding; standardized evaluation of programs; periodic evaluation of committees; filling research manager positions with scientists on a temporary basis; mechanisms to ensure adequate representation of national–international research (long term) interests. In universities there is a need for a shift in accent from individual to cooperative work, including graduate theses. A strategy needs to be developed within the research community to facilitate communication with the public and senior managers on long-term issues. Without an increase in the forces causing senior managers to be more responsive to the long term, the climate for research will remain as a perennial problem. This is because managers are conditioned by their role to think and act "short" in space and time, whereas scientists are conditioned by their role to think and act "long" in space and time. Development of an independent "scientific auditing" function, possibly coupled with existing financial auditing functions, is needed to improve the credibility of governments and industries in regard to resource interests that are "long" in space and time.

Key words: climate for research, limnology, management, environment, Canada, long term, basic research, applied research

Résumé

VALLENTYNE, J. R. 1978. Facing the long term: an inquiry into opportunities to improve the climate for research with reference to limnology in Canada. J. Fish. Res. Board Can. 35: 350–369.

La principale préoccupation qu'ont exprimée 125 scientifiques spécialistes des eaux douces lors d'entrevues individuelles est la détérioration du climat propice à la recherche. Les ruptures dans la continuité et l'ordre chronologique essentiels à la recherche sont le principal problème mentionné au ministère des Pêches et de l'Environnement (MPE); dans les universités, c'est le déclin de l'aide accordée à la recherche « pure »; et dans l'un et l'autre milieu, on note le manque d'attention accordé par les gouvernements et le public à des mesures visant à résoudre les problèmes à long terme. Nous analysons ces idées en fonction d'attitudes vis-à-vis de l'environnement, de la recherche et de la politique scientifique qui ont évolué de 1957 à 1976. Les suggestions précises visant à améliorer le climat de recherche au MPE sont les suivantes : l'application d'une politique touchant la recherche; le financement assuré sur une période de 3 à 5 ans; l'évaluation uniforme des programmes; l'évaluation périodique des comités; l'affectation des scientifiques sur base temporaire aux postes de gestionnaires de recherche; l'établissement de mécanismes pour assurer une représentation adéquate auprès des organismes nationaux et internationaux de recherche (à long terme). Dans les universités, il faudra déplacer l'accent du travail individuel vers le travail en collaboration, y compris les thèses d'étudiants postgradués. On devra mettre au point, au sein de la communauté scientifique, une stratégie visant à faciliter la communication avec le public et les cadres de gestion en ce qui a trait aux problèmes à long terme. Tant qu'on ne pourra intensifier le genre de pression susceptible de sensibiliser les cadres de gestion aux problèmes à long terme, le climat de recherche sera toujours l'éternel problème. Il en est ainsi parce que les gestionnaires, de par leur rôle, sont portés à penser et agir « court » dans l'espace et dans le temps, alors que les scientifiques sont, de par leur rôle, portés à penser et agir « long » dans l'espace et dans le temps. On a besoin d'instaurer une « vérification comptable scientifique » indépendante, possiblement couplée aux systèmes actuels de verification financière, afin d'améliorer la crédibilité des gouvernements et des industries en ce qui a trait aux intérêts « de longue portée » dans l'espace et dans le temps dans le domaine des ressources.

Received July 5, 1977
Accepted December 15, 1977

Reçu le 5 juillet 1977
Accepté le 15 décembre 1977

A charge of rape is easy to make, and sometimes made by a woman to protect her name; difficult to prove, and even more difficult to defend yourself against.

British legal experience.

Introduction

THIS paper is a description and interpretation of views pertinent to the climate for research that were expressed to me in individual interviews with 125 scientists involved in freshwater and estuarine research in Canada in 1976. It is also an explanation of these views. Through provision of background information on limnology in Canada I have attempted to make the account intelligible to persons from other countries and with different experience. My prime purpose was to examine the perceptual relationship between the mind of a scientist and the external world that impinges on it. Limnology and Canada were merely convenient vehicles toward that end.

Opinions on the climate for research are apt to be intensely personal. Because of this, reactions of readers to this paper may be emotional, and determined as much or more by job history and personality as by the author's words. It is unlikely that any of the persons interviewed would wholely subscribe to this paper as a statement of their perceptions. Nevertheless, most would likely agree that the issues raised are valid, and there is benefit in bringing them out into the open where they can be discussed and appraised.

The paper is primarily an introspective analysis of the research community. Although certain management strategies and institutional arrangements are suggested below, they are best viewed as incidental side-benefits rather than calculated products. My intent in undertaking the analysis was threefold: (1) to expose the concerns of scientists and research managers in terms of their ability to perform and direct high quality, relevant (in the long term) research; (2) to explain to persons unfamiliar with research why research is, and always will be, undervalued in terms of the benefits it offers to society; and (3) to alert the research community to opportunities and responsibilities that cannot be avoided if long-term science is to be maintained at its present level.

The factual basis of the study was derived from interviews with 62 scientists and research managers in federal laboratories, 44 professors and department heads at universities, 14 scientists and managers from provincial laboratories and research councils, and 5 scientists from industry. The interviews were conducted in six geographic areas (Halifax–Dartmouth, Montreal–Quebec, Toronto–Burlington, Winnipeg–Saskatoon, Edmonton, Vancouver–Nanaimo) from January to April 1976; at two conferences (Canadian Conference for Fisheries Research, Ottawa, January 1976; International Association for Great Lakes Research, Guelph, May 1976); and through letters and telephone conversations at various times. (See Appendix for a list of centers visited and persons interviewed.)

The approach used in these interviews was qualitative, subjective and intuitive, based on the experience of the persons interviewed and the interviewer. No attention was given to dollar budgets, man-years of effort or organizational objectives. These are often given undue attention by government departments and granting agencies because of their visibility, ease of quantification and susceptibility to manipulation. Other factors influencing the effectiveness of research of a more personal nature such as motivation, morale, and leadership, are typically neglected until some major disturbance or malaise arises, by which time it is too late for constructive action. Such situations are then commonly allowed to deteriorate one by one with serious, unmeasured and disregarded consequences to effectiveness in research. But, though the consequences may be invisible to the insensitive eye, they are nonetheless there, inexorably churning out their effects.

The analysis is presented in three parts. BACKGROUND attempts to place in perspective for non-Canadians and non-limnologists major changes that have taken place during the past 20 years in the practice and practitioners of limnological research in Canada. THE CLIMATE FOR RESEARCH is an evaluation of conditions for the conduct of long-term investigations in freshwater science in government laboratories and universities in Canada, based on information derived from interviews in 1976. OPPORTUNITIES FOR CHANGE deals with strategic opportunities to improve the effectiveness of research in limnology.

Three broadly similar reports were in preparation in North America at the same time as this study was in progress. The U.S. National Science Board (1976) Report, "Science at the Bicentennial," expressed the serious concern of U.S. leaders in science from universities, governments, and industries regarding the support and climate for scientific research. A report of the Environmental Research Assessment Committee (1977) of the U.S. National Research Council examined the need for research and the organization of research in a U.S. agency with comparable functions to certain parts of the Canadian Department of Fisheries and the Environment. The third (Fisheries Research Board 1977) was a broad review of aquatic sciences in Canada with policy recommendations. Several of the major conclusions of these reports were similar to those independently reached in the study on which this paper is based.

The definition of *research* in the context of this report is: work directed toward the resolution of practical problems of unknown or complex origin for which there is no reasonable expectation of solution within X years. Quite arbitrarily, for short-term research, $X = 0 - 3$; for long-term research X = more than 3. My definition of practicality is essentially that of Poincaré (1914): if there is a probability that a given event will recur at different times or places, research leading to an improved causal understanding of the event, whether

directly motivated with a practical end in view or not, is practical. The term *senior manager*, refers to a person who heads a group that encompasses wider interests than solely research; *research manager*, to a person who is the head of a research group; *manager*, to a manager of resource utilization or production; and *scientist*, to a person, typically with a Ph.D. or equivalent, who conducts research in university, government, or industry. *Research climate* refers to the sum of psychological factors affecting creativity in research.

Finally, I must stress to those unfamiliar with the process of research that the climate for research is a highly practical matter, easily subject to misrepresentation and misinterpretation. Trying to explain to persons who are not involved in research why it is important to think "long" in space and time is much like trying to convince a male why it is better to be female, or vice versa. Both functions are best viewed as complementary. The research community interviewed was not pleading a special case: it was fully cognizant of the economic times and did not regard itself immune to criticism and budgetary cuts. In expressing the body of its opinion through lifeless abstractions such as "research manager," "scientist," and the like, I have tried to put the accent where it is due, weighted toward opinions of the gifted and without minor qualifications.

Background

General

Canada has had a long involvement in aquatic research, first in fisheries with later extensions into oceanography and limnology. On a per capita basis, it can be claimed that Canada does as well in generating aquatic scientists as hockey players. This is perhaps best reflected in publications by the Fisheries Research Board (Carter 1968, 1973) of contributions from university, federal, provincial, and industrial laboratories. The history of the Fisheries Research Board in this and other respects has been summarized by Johnstone (1977).

Of the 45 universities in Canada, roughly one third are involved in freshwater research on a significant scale. There are two major federal centers for work on inland waters: the Freshwater Institute (FWI) in Winnipeg, Manitoba, and the Canada Centre for Inland Waters (CCIW) in Burlington Ontario; each has appreciable staff involvement in research, but includes regulatory functions as well. Provincial departments and research councils carry out research on inland waters and fisheries to varying degrees; the most prominent are in Ontario and British Columbia. Under the British North America Act, jurisdiction over most natural resources (e.g. water, forests, land) is allocated to the provinces. Fisheries, on the other hand, is a federal responsibility, delegated by letter agreement from the federal government to the provinces in some instances.

During the early 1970s, the federal government and most provincial governments created departments concerned with the environment or departments in which environmental and resource interests were combined. In the case of the federal Department of the Environment the following agencies were brought together in 1971: (1) the Department of Fisheries and Forestry, (2) the Fisheries Research Board (FRB) of Canada, (3) the water sector of the Department of Energy, Mines and Resources, (4) environmental health units of the Department of National Health and Welfare, (5) the Canadian Wildlife Service of the Department of Indian Affairs and Northern Development, (6) the Canada Land Inventory of the Department of Regional Economic Expansion, and (7) the Meteorological Service of the Department of Transport. These are now grouped into five Services of the Department of Fisheries and the Environment (DFE): Fisheries and Marine Service (FMS), Atmospheric Environment Service (AES), Environmental Management Service (EMS), Environmental Protection Service (EPS), and Planning and Finance Service (PFS).

Background information on the extent and development of limnology in Canada will be found in Frey (1963), a special issue of the *Journal of the Fisheries Research Board of Canada* (Volume 31, Number 5) prepared for the XIX Congress of the International Association of Limnology (SIL) in Winnipeg, August 1974, and the FRB Reports of Ricker (1975), Regier (1976), Harvey (1976), and Hamilton (1976).

Perspective, 1957–76

Participants in slow processes of major change are rarely aware of the extent to which change has taken place around them, and even less of the extent to which their behavior as individuals and groups has accommodated to that change. For this reason it is important as background to later sections to review some of the major changes that have taken place in the last 20 years affecting the practice and practitioners of freshwater research in Canada. The year of Sputnik, 1957, is a meaningful starting point. Sputnik came as a shock to political leaders in the United States, initiating new patterns of thinking there and in other parts of the world in relation to the support of scientific and technological research.

In 1957, ecology and limnology were unknown words beyond the small number of specialists who dealt with such matters. Neither the public nor governments were particularly interested in, or aware of, aquatic environmental and long-term resource problems. University staff complements in these areas were small and loosely coordinated, with little transfer of information beyond the scientific circles in which they worked. The typical environmental scientist in university avoided the study of polluted waters in the belief that it was somehow or other more important to derive an understanding of how nature operated under conditions free from the influence of man. Freshwater scientists worked as individuals, rarely as cooperative workers on teams. Species and communities of organisms were studied

TABLE 1. Number of Canadian members of the International Association of Limnology (SIL) at the times of its two North American congresses (Madison, Wisconsin, 1962; Winnipeg, Manitoba, 1974). The "unknown" category lists Canadian SIL members whose business address was not given in the membership list.

Year	University	Federal	Provincial	Industry	Unknown	Total
1962	24	11	14	0	2	51
1974	134	82	30	7	40	293

from a biological rather than ecosystem or limnological point of view. Computers and automated instrumentation were just coming into use. Modeling was virtually unknown. The title of the Science Council of Canada paper, "From Formalin to Fortran," nicely symbolized the transformations just beginning to take place (Larkin and Stephen 1971). To find an engineer, let alone an industrial representative, at a meeting of limnologists or hydrobiologists in 1957 was a curiosity.

Among Canadian universities, the University of Saskatchewan (Dr D. S. Rawson), Dalhousie University (Dr F. R. Hayes), the University of Toronto (Dr F. E. J. Fry and others) were generally regarded as the major centers of freshwater research, with the University of British Columbia on the rise (through the influence of Dr W. A. Clemens). Ontario was the leader among the provinces, the Fisheries Research Board (FRB) among federal organizations, and Beak Consultants Ltd. (which at the time had a total of four employees, including the President) among consultant industries involved in freshwater work. The employment of limnologists and freshwater hydrobiologists by industries was virtually unknown.

By 1976 the magnitude, focus, and national balance of effort had changed markedly. This is partly reflected in Table 1 which shows Canadian membership in the International Association of Limnology (SIL) at the times of its two North American Congresses. Canadian membership rose from 51 in 1962, to 293 in 1974, with a shift in proportions from different sectors. University staff and research effort increased in the early 1960s, accommodating to the increased flow of students generated by the post World War II baby boom. Engineers, physicists, chemists, geologists, and biologists freely intermixed at scientific meetings; many were working on the side with citizen-environment groups. *Ecology* and *biosphere* were recognized terms in newspapers, political slogans, and in the ink of high level economists and planners. Institutes of environmental studies, struggling for budgetary recognition independently of existing discipline-oriented departments, had formed at a number of universities. Citizen-environment groups were active in every part of the country, operating at a lower, less emotional, and more sustainable levels of activity than was the case in the late 1960s. Departments of the Environment, an unheard of thing in the early 1960s, were a feature of every major level of government.

Environmental consultant firms in Canada had increased vastly in number, some with total staff in the range of 50–150 employees. One person from the consultant industry estimated that there might be as many as 1000 biologists (part-time and full-time), active in a professional consulting capacity in 1975 as compared to a handful little more than a decade before. Hydro departments in two provinces, Quebec and Ontario, had added professional staff (20–50 man-years each) in limnology and freshwater hydrobiology. Some primary and secondary industries were in the process of following suit. Two major federal freshwater research institutes (CCIW and FWI) were in full operation. Scientists, engineers, legal experts, industrial representatives, and citizens were tangling in ways that would never have been anticipated in 1957. In short, the entire magnitude and focus of effort had changed.

Paralleling these visible and easily documented changes, new attitudes and modes of operation of research scientists appeared on the scene. Cooperative and interdisciplinary studies came to be recognized as a necessity of life, even though accommodation to group effort was jerky, poorly organized, and at times incoherent. In the 1970s antipollution research and applied research were no longer viewed with disdain and disrespect. The one-man show had lost much of its appeal. The motivation to play a role in defining and solving important scientific aspects of societal problems was firmly implanted in limnologists and freshwater hydrobiologists. The shift was in part statistical, not without some window dressing, and in no small measure due to the influx of a new generation of young scientists. Reflecting on the state of affairs 20 years before, no one could question that a profound change had taken place.

RELEVANCE AND RESEARCH

Political desire to increase the "relevance" of scientific research arose in a number of technologically advanced countries, including Canada, in the late 1950s and early 1960s. One aspect of this was the recognition of a need for greater effort in resolving environmental problems. This gave impetus to the development of improved measures for environmental protection and environmental research. Another aspect led to examinations of science policy (or lack thereof) with a view to achieving more direct, practical application from research. In Canada, this paved the way for the report, "A Science Policy for Canada," of the Senate Special Committee on Science Policy (1970, 1972, 1973), popularly known as the "Lamontagne" Committee, and in the United Kingdom for the Rothschild Report. In the United States the Office of Science and Technology was dissolved. The call came for greater relevance of science and technology in respect to societal needs and practical application. Relevance to a large extent meant *here and now*. It was in this context that a charge of irrelevance in research, particularly basic research, arose in the 1960s in Canada.

A charge of irrelevance in research has much in common with a charge of rape. It is easy to make, par-

ticularly by persons responsible for actions *here and now*, and has on occasion been used to enhance their image. It is difficult to prove, in that the time frame of application (typically 3–20 years, or longer) lies in the future. Who can prove irrelevance in what has not happened yet? And how can the research scientist defend himself against such a charge when the appropriate time for the assessment of relevance has not arrived? On top of all this the charge is not specific as to person, time, and place.

This is not to say that the relevance of current research cannot be evaluated *here and now*; rather, that a charge of irrelevance should not be lightly made or casually weighed by a scientific, public, or political jury. The remoteness of the time horizon of application and imprecision in exactly predicting the future make pronouncements on the irrelevance of research fertile ground for mischievousness and opinion rather than fact.

The effect of the political drive for greater relevance of scientific and technological research was beneficial in directing scientific effort toward the solution of important societal problems, but in application it has had two serious drawbacks that have been counterproductive and still persist. One of these was a failure to distinguish the time frame of application (short-term and long-term) prior to the question of relevance. The other was the uncritical acceptance of motivation (the categorization of research as "basic" or "applied" according to the intent of the sponsor or investigator) as the major factor in the application and applicability of research findings. A third factor has not helped the situation: the human tendency to discount the value of successful research. Who in North America, for example, is even aware of, let alone, attributes any value to the environmental research of the 1850s that paved the way for the eradication of cholera and other waterborne diseases? Successful research on practical problems erodes its own support base.

The failure to distinguish the time frame of application prior to considering the question of relevance has led, at least in federal laboratories concerned with aquatic environmental research, to an accent on short-term research with the promise of immediate, site-specific benefits. But the sum of a number of site-specific, project-oriented studies does not automatically lead to the development of generalized solutions applicable to other times and places. The development of such solutions, i.e. the science, must take place in its own right. If it does not, practicality is inhibited. The result is then not even beneficial in the short term, quite apart from the cost of reduced long-term payoff because of diversion from development of generalized solutions. Short-term problems stretch out. Eventually, we may find ourselves at the end of the limb.

The second confusion arose from use of the terms *basic* and *applied* as though they were mutually exclusive. The Lamontagne Committee defined *basic* research as "research aimed at extending the frontiers of knowledge." The Committee recognized the importance of *basic* research, but it repeatedly equated this to "curiosity-oriented" research and questioned its relevance to the development of technological innovations in industry and the national goal of economic growth.

The Lamontagne Committee would have been wiser if it had recognized, as did Henri Poincaré (1914) in the initial chapter to his "Science and Method," that "curiosity-oriented" research or "science for science's sake" is a fiction. Scientists do not collect facts or study relations randomly. The most interesting facts and relations are those that have a chance of recurring; and it is in this recurrence that the great practicality of science lies. Most scientists would rapidly wind up in mental institutions if it could be proved to them conclusively that their work had no practical application; i.e. that no one would ever use their work again. The Committee thus confused motivation and applicability. It also failed to recognize the extent to which its assumptions and recommendations were dependent on a more penetrating analysis and detailed understanding of how practical innovations arise in science and technology.

Comroe and Dripps (1976) provided such an analysis for the 10 most significant clinical advances in cardiovascular and pulmonary medicine and surgery in the past 30 years. Defining *basic* research as research on mechanisms of action, they found that 62% of the key background contributions judged to have been essential to the development of these major clinical innovations in the opinion of a body of experts was basic research *at the time it was done*. Furthermore, 41% of these key background contributions were not even clinically oriented at the time the work was done. The authors concluded that: "basic research, as we have defined it, pays off in terms of key discoveries almost twice as handsomely as other types of research and development combined." These findings document the need for development of an understanding of how the system of science and technology actually works in terms of giving rise to practical innovations, with a redefinition of terms and a fresh look at science funding strategy.

The call for research that finds application in the hands of some identified client *here and now* has also led to a decline of strategic, multiclient-oriented research. Beverton (1974) pointed out the fallacy of this in respect to research for which there will be customers *everywhere and later*.

A cybernetic analysis completed in 1975 of activities within the Fisheries and Marine Service, DFE, recognized the virtues of a division of expertise according to time frame. Functions were grouped into "reds" (immediate action with short response times) and "blues" (delayed action with long response times), broadly comparable to what had earlier been referred to in DFE as "operations" and "research" groups. A third category of "purples" might have been invented, corresponding to the mixed response times required in many environmental impact assessment programs: how-

ever, it could also be argued that this function, like the color, is really a mixture of two primary functions.

The effect of pressure for greater relevance *here and now* on the part of the "blues" in government-based research has squeezed and distorted the time frame for research. While this pressure may be useful in shortening the time between discovery and application, it becomes counterproductive when the "blues" are pushed to a point where, through lack of adequate preparation time, continuity, and moral support for research, they begin to perceive ineffectiveness in their own work. When this happens a research laboratory becomes self-destructive. The gap between managers and scientists widens. Opportunities for work elsewhere come to be viewed in a favorable light. The quiet, self-assured scientist goes off in his corner, and continues work that he knows is scientifically well-based and relevant. The more aggressive seek out opportunities to ridicule management decisions and take to writing derogatory memoranda on what they perceive as misguided, changing, and meddling directives from above. The less aggressive and less self-assured resort to closed-door or hushed, hallway conversations with eyes attentive to whoever may be watching, wasting time discussing rumored actions that may or may not materialize and may or may not affect them; they take on the characteristics of displaced persons, *displaced in time*.

Persons unfamiliar with the modus operandi of research workers may find it difficult to appreciate the importance of continuity and time frame as factors crucial to effectiveness and "relevance" in research. The scientist is programed through training and occupation to think long term. The Ph.D. degree, the union card for entry in the profession, typically requires 5 years beyond the Bachelor's degree. The time for problem formulation of a new research project, if it is to avoid redundancy on an international scale, demands 6 months or more of intensive effort involving reading, consultation with other workers in the field, and just time to "think the problem out." The design, analytical, and reporting phases of a well-planned investigation typically require 5–10 times the intellectual effort spent on the data acquisition phase. In all, a minimum of 3–5 years is typically required in imaginative research to proceed from problem conception to a final report. For highly imaginative work the time frame is even longer.

All this is well recognized by those skilled in research. Any distortion of continuity and time frame through repeated interruption or redirection of effort must inevitably exact a penalty in the quality and relevance of research, particularly long-term research. No amount of pressure or coaching will convert a proven marathon runner into the winner of one 100-metre race, let alone 400 races. Nor is the reverse likely to be true.

The importance of research climate should not be undervalued merely because it is a subjective and perceptual relationship between a scientist and the external world as he, or she, sees it. There is an element of the artistic in it that permits the research worker to perceive problems before they become apparent to the rest of the world. Research climate is infectious: when activated it inspires or kills. If we gave the same inattention to physical climate in our lives as is given to research climate in our laboratories, we would justly be regarded as fools. Perceptive scientists in unfavorable laboratory conditions are like persons with asthma. They have no need of instrumentation to tell them what research climate is or how it affects their work.

The Climate for Research

General

On the basis of preliminary discussions with a number of limnologists and hydrobiologists from government laboratories and universities in the preinterview phase of this study, it became clear that the predominant concern was over a deterioration of climate and conditions for effectiveness in research. One aspect of this concern centered on disruptions to research in federal laboratories as a result of diversion of scientists to management or "firefighting" (i.e. localized) activities. This concern for the quality of research in federal laboratories was not only cited by scientists within federal laboratories, but also by some university staff as well, particularly those with contacts or experience in government laboratories.

Among university professors the main issue centered on the national climate for research as perceived from statements of high government officials; and attrition, primarily through inflation and diversion to other activities, of governmental support for "basic" research.

A third "climatic" concern was significant by its absence in discussion with all but three of the persons interviewed (one from a university, one from a government research laboratory, and the third from a mixture of the two): a need to get the scientist out of his particular laboratory and area of expertise into interdisciplinary, cooperative work in unfamiliar circumstances.

It is important to stress that in my interviews with scientists and research managers in governments and universities, I made no attempt to lead into a discussion of research climate. After explaining the nature of my assignment, my initial questions were (I knew many of the persons interviewed from one or more previous contacts): "Well, how are things going?" "Any problems?" Or, "What would you like to talk about?"

Under normal circumstances one might have expected the response to be something like: "Not bad. Hey, do you know what we're working on now?" Or, "Have you seen my paper on . . .?" Instead, interviewees typically commented on the failure of governments to address themselves to important long-term resource problems, and deterioration of their ability to focus on research. For one university professor, who I had never met before, it was enough to know that I was a "government man" to trigger accurate machine-gun fire.

The analysis that follows is presented under three

TABLE 2. Number of different titles and leaders of organizational units above a typical scientist at the Freshwater Institute (FWI) and the Canada Centre for Inland Waters (CCIW) from 1969 to 1976.

	No. of titles of organizational units — 69/76		No. of different leaders — 69/76	
Level of organization/Role	FWI	CCIW	FWI	CCIW
Department/Minister	4	3	3	4
Department/Deputy Minister			3	3
Service/Assistant Deputy Minister	2	2	2–3	3
Region/Regional Director General	0–1	0–1	0–1	0–1
Institute or Centre/Director	2	1	3	2
Division/Leader	2	2	1–2	2
Section/Leader	2–3	2–3	2–4	2–4
Project/Leader	1–3	2–3	1–3	1–3
Totals	13–17	12–15	15–22	17–22

headings: the problem as perceived by research workers in federal laboratories; the problem as perceived by professors and department heads in universities; and getting the most out of the scientist.

FEDERAL LABORATORIES

The Canada Centre for Inland Waters (CCIW) and the Freshwater Institute (FWI) jointly account for the bulk of federal activity in freshwater research. Much of the following discussion is centered on them for that reason. It should not be presumed that they are unique among DFE research laboratories in respect to the issues discussed under this heading. If I accent them here, particularly the Freshwater Institute, it is only because I am most familiar with their circumstances.

Both centers physically came into existence in 1966, to some extent from preexisting groups, but in part due to demands for research and monitoring relative to the investigation of pollution problems in the lower Great Lakes under the aegis of the International Joint Commission. The FWI was established through transfer of fisheries and technological personnel from London, Ontario, and recruitment of new staff to develop an improved understanding of manmade eutrophication and mechanisms for its control in the lower Great Lakes. The CCIW was established through transfer of physical sciences staff from Ottawa and the recruitment of new staff to monitor water quality and assess transboundary pollution in the lower Great Lakes.

Here is what has taken place around scientists who worked at FWI from 1969 to 1976. The organization they worked for changed from The Fisheries Research Board to the Department of Fisheries and Forestry, to the Department of the Environment, and then to the Department of Fisheries and the Environment (DFE). In some cases they do not even know now whether they are part of Fisheries Management or Ocean and Aquatic Sciences sector of the Fisheries and Marine Service. The Institute they worked in has retained its name, but the meaning of the name changed from that of a research unit to a building. All of the sections in the Institute have had at least one change in name. They have worked under four different Ministers, three different Deputy Ministers (DM), three different Assistant Deputy Ministers (ADM), three different Ottawa-based research directors or equivalent, and three different directors of their Institute. None of the section leaders there in 1969 remains in a managerial role in the Institute. Subsection leaders have changed at least once in the typical case. On top of all this, their unit, which once had a national identification, has been regionalized and their employment status changed from employees of a government board to public servants.

The history of organizational names and leadership above a hypothetical scientist at CCIW, originally set up under the Department of Energy, Mines and Resources, differs from that at FWI only in minor detail. The only significant difference is that all CCIW staff (except for a small FRB group) were public servants from the start.

Activities at the two centers were further complicated by satellite groups: a biological satellite group of FWI at CCIW, and a physical sciences satellite group of CCIW at FWI. The FWI satellite originally reported to its parent body in Winnipeg. In 1972 it was renamed the Great Lakes Biolimnology Laboratory and identified as a separate responsibility center reporting directly to Ottawa. In 1974, CCIW satellites in Winnipeg and Vancouver were brought under regional, rather than CCIW control. The original CCIW satellite at FWI has had three leaders (1969–76); the FWI satellite at CCIW, four. The numbers of different organizational names and leaders above typical scientists at the two centers from 1969 to 1976 is shown in Table 2.

Over the same time interval there has been an increase in length of the chain of command. At FWI this was from Director — FRB Chairman — Minister, to

Director — Director-General — ADM — Senior ADM — DM — Minister, with the same opportunity for error as in the game of communicating a message through individuals in a circle.

Many managers might regard the above situation as nothing particularly unusual. Perhaps some would even say that it is healthy to change managers periodically so they don't become stale in their jobs. But there is a heavy cost to this when the frequency of managerial changes approaches or exceeds the necessary readjustment time. Uncertainty, with all its handmaidens, precedes and follows such changes. A shift in name and leadership at each level typically brings in a suite of new objectives, new committees, and administrative arrangements designed to filter down the chain and give evidence of a "forwardlooking," "action-oriented" approach.

Yet these do not constitute the major evils in the eyes of the scientist: it is the implied lack of commitment to problem resolution, the lack of organizational objectives to which scientists can relate, a perceived managerial neglect of research needs, and sometimes the senior manager's ignorance of research proceeding under his own command. In addition, there is a lack of responsibility and accountability when the initiators of actions do not remain to reap the produce of the seeds they have sown.

What were the problems cited in the inerviews? The most common references were to: lack of direction and changing directives from above; the request from Ottawa or the laboratory director, "Can't you do something on so-and-so?" without saying what, or even asking the extent of the problem (e.g. mercury in 1970); the increasing difficulty of communicating to the "top" with lengthening of the chain of command; frustrations with management; local and national leadership, inattentive and unresponsive to the research mind; reorganization to suit personalities rather than problems; antiresearch statements of high level government officials; a deep belief that make-or-buy policy (discussed below) is going to put government science out of business; poor formulation of charges to committees; ineffective use of committee members and their time; lack of confidence and respect for superiors in their ability to think and act with due regard to the long-term; being pushed into unimaginative, quick-and-dirty research; fire fighting; political inattention to long-term resource issues; disbelief and disgust at the extent of inter-Service territorial fighting. To sum it up: *a feeling of being unneeded, unwanted, misunderstood, and misused; and, in addition, threatened by a communal charge of irrelevance in research.*

It is difficult to quantify the responses in terms of major areas of concern because of differences in the experience of the persons interviewed and the lack of a standard format in the interviews. But if one were to classify the responses to the general questions raised in this section as emotional, serious, or indifferent, approximately two thirds of the responses from federal scientists and research managers would fall in the first class, one third in the second, and almost none in the third. It is noteworthy that these concerns not only stemmed from scientists; *they were, in fact, often more eloquently and vehemently expressed by research managers*.

Somewhere along the line it becomes pertinent to ask whether these frustrations and the phenomena of multilevel reorganization, musical chairs, and changing (even cyclical) directives are appropriate to the conduct of investigations typically requiring a minimum of 3–5 years from planning to completion. Is it any wonder that scientists and research managers are skeptical about the direction of long-term science?

At the same time, if conditions have been that bad, why haven't more scientists left? (Of course, some have.) Apart from the usual factors of habit and circumstances that mitigate against change, I believe there are three counterfactors at work: research in DFE laboratories has been well supported in terms of assistants and facilities (an important factor for persons with a primary interest in research rather than teaching); scientists' salaries in the civil service have been statistically competitive with those in universities; and job opportunities elsewhere have not been plentiful (though the best scientists rarely lack the opportunity to move). This does not say that because one part of the body is healthy, another can be ignored.

It is also pertinent to speculate whether the responses would have been any different if the interviews had been held 10 or 50 years ago. In all frankness, I suspect that many might have been the same. But one aspect was unusual and significant: *the sometimes dejected, emotional, and (on one occasion) belligerent nature of the responses.*

One might also ask how much the frustrations and disenchantment cited above are due to various factors, such as: rising aspirations for the societal significance of environmental work; intralaboratory vs. extralaboratory factors; the lack of clear departmental policy on research; the regionalization of research; getting pulled apart by an overwillingness to take on jobs; increased work load due to greater governmental involvement in environmental problems; among former FRB personnel, the recollection of more suitable circumstances for the conduct of long-term research; too extensive penetration into laboratories of the interface between politics and science, with the director or director-general trying to prethink the Deputy Minister or politician; job classification and the research scientist appraisal system; the inevitable consequence of a rapid buildup of staff and facilities; and others.

I am not inclined to guess the relative importance of the above; however, some observations are pertinent to any interpretation:

1) There was no single authority (role or person) in DFE or FMS in 1976 that acted as a leader and spokesman for research. Neither the DFE nor any of its Services had an explicit policy on long-term research.

Incredible as it may sound, there was no clear definition of a policy role for science in DFE.

2) The scientists and research managers interviewed in 1976 perceived a deterioration of their ability to contribute to the resolution of environmental problems. Everyone seemed to look "upward" for the source of the problem, rarely downward or internally; however, a hunt for scapegoats will solve nothing. The central question is how to foster the vitality, continuity, and time frame essential to assure the relevance, particularly in the long term, of research.

3) The perception of an adverse climate for research was neither peculiar to federal laboratories involved in freshwater science, nor to FMS or old FRB laboratories. It was present in all DFE laboratories visited. More than that cannot be said from the information gathered in this study.

4) Many (not all) scientists involved in work with the International Joint Commission (IJC) found that work more satisfying and less frustrating than work conducted totally within DFE, particularly when the latter involved Service interactions. In other words, federal–provincial and Canada–United States interactions under IJC tended to be perceived as coming about more easily and with fewer frustrations than interactions between the various Services of the Department. The significance of this is discussed below.

5) In 1976 no organizational arrangements for national or international communication and consultation, either intergroup or intragroup, existed among senior scientists, research laboratory directors, or senior officials of the Department on major science issues. With such arrangements, it is likely that the climate for research would automatically improve.

Universities

The perception of research climate problems in universities differed from that in federal laboratories in that it pertained more to the national climate for research, rather than local working conditions.

This is understandable in that the university professor has more direct control over his personal activities in research than scientists in government laboratories. No one is likely to identify himself as a problem. Also, the primary raison d'être of the university professor is to provide guidance and instruction to the young or uninitiated rather than to conduct research. Research is a necessary adjunct to higher learning, but not the primary condition of employment as with scientists in government laboratories.

The concerns that emerged from discussion with university staff centered on perceived government policy on scientific research, particularly *basic* research. It is difficult to summarize the collective sense of these concerns, but if one had to put it in a nutshell it would be the perception of a failure of governments to address themselves to long-term resource-base and environmental problems and to reflect these concerns in an acceptable policy for long-term research, particularly *basic* research. *Basic* research in these discussions did not mean nonapplied or "curiosity-oriented" research. It meant research conducted with a view to improving the understanding necessary for the resolution of long-term problems. Among various specific concerns cited were: public statements from high government officials questioning the importance of research; a perceived failure of the federal government to appreciate the practical importance, in the long-term, of *basic* research; the severance of government research boards (Fisheries Research Board, Defence Research Board) from direct control over research in their areas, and the feeling that the National Research Council would be next to fall; the attrition, through inflation, of federal support for *basic* research in universities; deterioration of staff and climate in nearby federal laboratories; the unsuitability of contract research (and poor problem formulation therein) for student training programs because of restrictions in time and scope; and the effect of declining real support for research on the motivation of young people, particularly students and young faculty members. About one third of the persons interviewed were emotional (to varying degrees) in stating their concern.

One of the problems referred to by some university staff was the difficulty of setting up interdisciplinary resource management programs in the face of vested disciplinary (departmental) interests. Where interdisciplinary training programs exist they are often restricted to the Master's level and often not supported with sufficient "hard" funds to get them off the ground. The Westwater Research Centre, University of British Columbia, seemed to be generally regarded as one of the few success stories, though perhaps more for faculty than student involvement. The Institut National de la Recherche Scientifique-Eau (INRS-Eau) of the Université du Québec also has the seed for success if its financial base could be strengthened. Although the problem of initiating interdisciplinary work in universities was never mentioned in the context of research climate, I have the distinct impression that it is comparable to some of the climate problems discussed in connection with government laboratories. The perceived obstacle is an "unreal" discipline or department instead of a nonscientific bureaucracy.

One university department head commented on the increasing inability of universities to produce graduates with background and experience fitted to cooperative, interdisciplinary work involving the sophisticated tools available in government research operations. Taken in conjunction with the previous paragraph this suggests the desirability of flexible, experimental cooperative training enterprises involving government and university expertise. Canada is at least a decade behind the United States in this regard; viz. the quasi "research universities" evolved through Carnegie, Rockefeller, and Wood's Hole establishments. With a more flexible accent on gifted people, rather than organizations, we could perhaps jump ahead. There is considerable doubt in my

mind that any established university can effectively evolve in this direction. I have even less confidence in traditional government departments to take the lead. But with a flexible, in–out arrangement for the imaginative talents of both, and support from "above," something just might work.

GETTING THE MOST OUT OF THE SCIENTIST

One of the more significant aspects of the interviews was the almost complete lack of reference to the scientist or university professor as a resource in need of change. Only three persons interviewed expressed any concern in this area. One was a federal government research manager. His concern was how to pull the federal scientist out of his laboratory to interact with provincial counterparts. As noted above, one university professor and department head commented on the growing disparity between the type of research training in limnology and freshwater hydrobiology provided in universities (one student working alone, limited equipment, small scale) and the research in government and consultant laboratories (cooperative interaction among many workers, major equipment and facilities, large scale) where students are increasingly likely to find employment. A third person, on leave from university and working a large-scale government project, stated the problem this way: "How to get good men working on real problems."

The lack of reference of the scientist to himself as part of the problem is not surprising in view of the biological preoccupation with "me" and the human tendency to look for scapegoats when faced with personal problems. But it is surprising in the sense that research climate is a *relationship* between a scientist and external forces that impinge on his performance in research.

I believe there are two factors at the root of the problem (in addition to the lack of cooperative education discussed below) both of which arose as adaptations to societal needs: the accents on the long-term and specialization. Society long ago recognized the practical importance of long-term thinking, planning, and knowledge development; it institutionalized them in the form of universities, research institutes, and planning groups at various levels of government and industry. In this sense it is accepted that workers in these institutions should have their "heads in the clouds." Secondly, the practical advantages of specialization, in its collectivity, were recognized and put into practice by society long before Adam Smith enunciated the principle of the division of labor or Emile Durkheim saw its significance as an adaptation to social life. These virtues are now impediments to the effectiveness of research. We have reached a stage where communication is the key to support for research; a task perhaps ill-suited to specialists with their heads in the clouds.

The solution is not to reduce the accent on long-term thinking or specialization. To do that would be socially, economically, and individually destructive. The solution is to create new lines of communication and improved feedback between the parts and the whole. The scientist must take the initiative in this. If not, actions will be taken by others that, through accident rather than design, will be divisive and destructive.

The main problem lies in improving the interaction among three communities of interest: scientists (in universities, governments, and industry), senior managers (politicians in governments, resource managers in government and industry), and citizens (users and controllers through votes). For the mix to be socially effective, each component must communicate with, and be in part directed by, the others. A view from within one segment that avoids the others is bound to be distorted. The question is how to break through the communication barriers.

A case was made earlier in this paper for the protection of long-term research from interferences destructive to its effectiveness in the long-term; i.e. to keep scientists productively working on imaginative research by insulating (not isolating) them from undue interferences. Now attention is focused on initiatives that might be taken within the research community to improve the effectiveness of that community in the resolution of long-term problems. This demands improved communication from scientists to managers and citizens. There is no conflict in this. The whole thing hangs together or not at all.

The problem in bringing this about has already been stated. The very characteristics that society has nurtured in scientists, specialization and accent on the long-term, are impediments to communication. Time has shortened and specialization is extreme.

But scientists do not look at it this way. They regard the problem as external: a failure of governments and people to be responsive to long-term issues, and interferences to their effectiveness in long-term research. With considerable legitimacy they regard any major departure from their areas of specialization as social and personal misuses of their time.

A comparison between environmental science and medicine may make this discussion more concrete. The counterpart of the environmental scientist in medicine is not a practicing M.D., but a medical research worker. Both medical and environmental research workers create opportunities for improved health by discoveries and inventions that are put into practice by others. There is no personal life-and-death bond between medical or environmental scientists and society as there is between a practicing physician and his patient. The public cannot sense environmental disorders as readily as an individual does disease, particularly when we invest most of our effort in controlling symptoms of problems rather than causes.

It is this absence of a personal bond that makes the link to the public vital to the support of research. The environmental research community has no recourse other than to invest some of its time in promotional and mass educational functions. To do otherwise would

be self-destructive and socially destructive. It does nothing to single out government or industry as scapegoats when it is realized that they are subject to social controls and citizen votes.

The problem is that there has been no strategy in operation within the research community to overcome the major constraints to communication — the accents on long-term and specialization. Things have been left to handle themselves.

But they won't! No amount of rhetoric will ever convince a concert pianist that either she or society will benefit from a switch to the violin or public relations work. Nor will a Canadian tennis champion be persuaded that he should go in for hockey because it is a more popular national sport. The key to change lies within the research community itself. Direction and pressure from outside will only be counterproductive as evidence presented earlier has shown. The problem is not peculiar to environmental science; it is a general problem of research.

If a continuing low-level strategy to get scientists professionally interacting outside their specialty and organization were rigorously pursued, it would pave the way for "getting good men to work real problems" in the societal sense. With a rationale, defined limits, adequate warning, and knowledge that all are being-treated alike, scientists are reasonable persons. They can be diverted to any function for an hour or half day once a year. A few days per year will not create serious concern even if the diversions are only indirectly related to their work. A week per year demands more obvious connection with group or individual responsibilities. A month brings considerable resistance and must have direct relation to the capabilities and obligations of the individual and group. In addition, firm assurance must be given that the assignment will not stretch out or make the individual more prone to similar assignments at later times. Commitments of several months or years to "fire-fighting" activities or managerial roles will be greeted by a negative response unless directly related to individual talents, which is rare. One of the major hindrances to all this is that managers unskilled in science and research do not know the strengths and weaknesses of scientists that they can exploit.

In crisis situations there is no difficulty in obtaining a positive response from most scientists. Experience in DFE with mercury, elemental phosphorus in Placentia Bay, and NTA has shown this. Cooperation is more difficult to obtain when the needs are of a less serious nature or when time commitments are made from above solely to protect territorial interests of the institute, service, or department.

University faculty have a key long-term role and responsibility in all this. Most of the habits, aspirations, and behavioral characteristics of scientists are fixed by the time they emerge from graduate school; some long before that. Yet, the recalcitrance of university faculties to change is notorious. The territoriality of university staff in relation to vested personal or departmental interests and teaching responsibilities is an even stronger force than found among scientists in government.

Opportunities for Change

Improving the Climate for Research in DFE Laboratories

It should be abundantly clear from the previous section that in 1976 the scientists and research managers in DFE interviewed in this study were dissatisfied because of constraints to the effectiveness of their research. The manner in which this information was presented to me suggests that senior managers and the research community of DFE would be well advised to give this problem the same attention they would devote to the collapse of a major fishery, a large oil spill in one of the Great Lakes, or problems associated with more than 0.5 ppm of mercury in fish. It is noteworthy that this problem was anticipated by Needler (1974) and that it is not unique to Canada (see National Science Board, 1976; Environmental Research Assessment Committee, 1977).

In my opinion, there will be no solution to this problem without a clear statement of the long-term objectives of DFE, a policy on research, and creation of a budgetary unit in DFE for long-term interests in planning and research. Essentially, the same conclusion has been reached by the Fisheries Research Board (1977).

Program Continuity in Long-Term Research

Firm assurance of continuity of research programs within DFE and its laboratories is rarely, if ever, given beyond a period of 1 year. Of course, this is an exaggeration in the sense that there is practically a lifetime commitment to a scientist once employed, barring unacceptable work performance or redundancy. It is also an exaggeration in the sense that commitments are made to long-term research on persistent problem areas in cases where it is recognized that a problem cannot be solved in less than 1 year. But these commitments are not binding on managers. New circumstances have a habit of entering in, requiring interruption, reassignment of staff, or termination of the program for more immediate needs.

This matter is critical in long-term research programs involving group effort, particularly when individual participants come from different organizational units in the Service, Department, government, or nation. The only effective vehicle that carries a virtual guarantee of support for inter-Service research programs beyond 1 year is work under a reference submitted to the International Joint Commission. The time frame in those cases is typically 1–5 years.

This is a ludicrous situation. The effects of clear-cutting or reforestration programs on a river basin cannot be evaluated in less than 5–10 years. The effects of a given loading of pollutants or implementation of some control measure on an aquatic ecosystem likewise re-

quire a comparable time if the year-to-year influences of extraneous factors are to be adequately taken into account. Evaluation of changing management practices on fisheries and water bodies must be tuned to the regeneration times of the populations, communities, and water masses involved.

To say that governments cannot fund research on a long-term basis is an evasion of responsibility. The problem should be stated the other way around: if long-term interests are recognized as an essential component of government activity, then institutions should be created within it for funding on time scales appropriate to the work involved. It is significant that approximately half the funding of the National Research Council of Canada is made on the basis of binding 3-year commitments. Why is the federal government prepared to do this for universities, but not for what is presumably more practical work in its own departments?

If the Department or federal government does not find institutional mechanisms to provide assurance for the support of long-term work, it will not have the information base necessary to understand and resolve problems in the long term. It is just as simple as that.

Technical Evaluation of Effectiveness of Research

There are no effective, uniform procedures for the evaluation of scientific research programs (or for that matter, any other aspects of any programs other than financial) in DFE laboratories. An effective annual, internal peer review system has been in operation in FWI for some years and a comparable system has been set up at the Pacific Biological Station (PBS), Nanaimo, B.C. Somewhat looser arrangements have been in operation at CCIW, including a process for external review that fell into disarray after a few years because of the reluctance of separate Service units at CCIW to agree to the process. I am not fully informed of the extent to which comparable arrangements to those at FWI and PBS may exist in other research laboratories of DFE, but I have reason to believe that they do not exist to the same degree. DFE should have systematic procedures in place for evaluation of the effectiveness of its work, both research and operations. The present system is like setting up a chain of restaurants without a system for quality control.

Peer review and evaluation are essential to effective performance in research. They are particularly crucial to the termination of ineffectual programs that have lingered beyond their time. They provide an opportunity to bring before the director of the laboratory existing problems and new approaches that he might otherwise disregard or not be aware of. In addition, reports on past progress and new proposals provide a forum within the laboratory for feedback and discussion, permitting workers to see how they fit into the whole.

There are two needs: one for a systematic, annual, internal evaluation with reporting to and feedback from the director; the other for periodic (4–5 year), external evaluation with reporting to and feedback from the senior management of the Service or Department. The model for the latter is the National Research Council of Canada or U.S. National Science Foundation review committee structure that moves in and dissects a laboratory from top to bottom. This is a common and accepted procedure in federally supported research operations in government and university laboratories in the United Kingdom and the United States. The lack of an equivalent in Canadian federal establishments is incredible.

The Department should implement both types of evaluation systems on a permanent basis. The time cost per laboratory in each case is equivalent to less than one man-year of review effort distributed among five to six people, with an equivalent total time involvement from laboratory staff. The known benefits far outweigh the cost. The need for such evaluation is by no means limited to research.

Committees and Meetings

DFE is recognized as unusual in the extent to which subdepartmental allegiances and constraints reduce the effectiveness and image as a department as a whole. A certain amount of territorial protection is a normal and healthy component of any hierarchical structure; however, there are limits in the extent to which this should inhibit scientific responsibilities that transcend the individual parts.

In many (not all) committees and task forces within DFE, Service constraints enter at too low a level and too early a stage to permit fundamental environmental issues to emerge in a form appropriate to effective resolution at higher administrative and political levels. Part of the problem, as pointed out earlier, is that there is no single *national* spokesman or leader of research in DFE. Taken in conjunction, these two factors exact a heavy penalty in terms of the ability of DFE to grapple holistically with long-term environmental problems. They prevent fundamental scientific and technical issues from reaching the highest political levels in a form that does not anticipate the role of the political process in problem resolution. And the accent on territorial protection erodes the effectiveness and morale of scientists.

As noted above, a significant number, not all, of DFE research scientists found work under IJC more satisfying than inter-Service work under DFE, even though the primary role of IJC is not research. Part of the reason for this lies in good problem definition, part in the politically strong terms of reference of IJC, and part in the nature of the participants themselves (e.g. persons not primarily oriented toward long-term research).

A functional classification of task forces and committees in DFE would reveal many different types, some designed for information exchange, some for problem definition, some for problem resolution, etc. Discussion

is restricted here to issues that transcend individual Service mandates, nationally or regionally, for which groups are set up to examine and report on some particular problem or set of questions of a complex, nonroutine nature. The effectiveness and image of the Department as a whole would be vastly improved if recognition were separately given to *departmental* and *inter-Service committees*, with members appointed as individuals from Services in the former case and as representatives of Services in the latter case. The former procedure is used routinely and effectively by the International Joint Commission. Even the Commissioners themselves are not appointed as national representatives.

The appointment of individuals from Services to *departmental committees* obviously does not mean that the individuals are freed in one fell swoop of Service or other organizational constraints. To do that would be impossible, unrealistic, and undesirable. What it would do is to allow the individuals to operate as a single body in the joint interest without being totally bound by organizational constraints. If the International Joint Commission tried to operate without this protective device, the states, provinces, and two federal governments would be at odds with each other from the start. *I can think of no single measure that would better allow the Department and Minister to grapple holistically with complex environmental problems than adoption of this simple procedural mechanism.*

There is need for periodic review and evaluation of DFE involvement in committees, subcommittees, task forces, and the like in terms of number, composition, efficiency of operation, and the effectiveness of individual members. Committee and task force members are to committee and task force functions as scientists are to research projects. If the members and functions of committees were evaluated with the same depth and intensity as in annual reviews of research projects at FWI and the Pacific Biological Station, considerable savings in man-years of effort and travel expenditures would unquestionably result. There should be a periodic review process that assumes dissolution of all committees without justification. Care should be taken to assure that these reviews and evaluations are carried out by persons with experience and insights into the nature and needs for the functions.

National and International Focus

There has been no effective national integration of research functions and programs in DFE since its creation in 1971. Following transfer of FRB staff and facilities to FMS in 1973, there has been no effective national integration of research functions and programs in FMS.

This lack and even dissolution of national and international focus on environmental research at a time of heightened interest in national, international, and long-term aspects of resources and the environment is extraordinary. It is of interest that at the same time as these changes were taking place in Canada, exactly the opposite course of action was recommended in the United States (see appendix to Environmental Research Assessment Committee 1977); and that the Fisheries Research Board (1977) has separately concluded that a need exists for a separate national identity for research on fisheries and aquatic sciences in DFE.

If this unusual situation persists — as it may, for other reasons — steps must be taken to ensure that national and international research interests and obligations are adequately addressed, and that the regionalization of DFE activities does not foster duplication within DFE and with provincial responsibilities. Quarterly meetings of the directors of research laboratories to discuss common research needs in a national context would be of value.

Scientific Leadership of Sections

The classification of group leaders at levels immediately below the director of a laboratory as research managers, with the implication that they are out of active research, is counterproductive. An analogy can be made to a football team, recognizing the obvious difference that scientists can look forward to a lifetime career of active play, whereas football players can not. Based on this analogy, the director of a research laboratory is a coach; the principal section leaders under his direction are quarterbacks of research teams. The scientists are the players. The designation of section leaders as research managers is counterproductive to getting good leadership. It would be more advantageous to appoint scientists as section leaders for limited terms on the presumption of nonreappointment, as is often done for department chairmen in universities. This would permit greater flexibility in cases where performance is less than desired (an easy mechanism for removal without loss-of-face); it might also help to attract scientists to leadership roles, avoiding the traumatic decision of severance from an active role in research. It is significant that sectional leadership at FWI and CCIW actually changes at intervals of approximately 3 years.

The reasons why it would be advantageous to appoint section leaders for limited terms on presumption of nonrenewal of the appointments were succinctly stated by one interviewee (Dr Michael Healey, Pacific Biological Station, Nanaimo): "(1) more people would get a chance to experience the real frustrations of research administration, and that should improve the understanding between management and research; (2) because the manager would be expected to resume active research in the near future, he would be eager to keep in touch and research would remain a high priority item with him; (3) it would reduce the 'them' and 'us' syndrome in managerial hierarchies; (4) the trend to bureaucratization of managerial positions would be slowed; (5) senior managers would have to get to know their whole staff better, not just a favoured ruling clique."

Laboratories could give recognition to these facts of life by making section leader appointments as scientists

with extra duties for a limited period of time such as 3 years. Alternatively (less desirable) scientists could be appointed as research managers for limited terms. In either case, leadership evaluation should be based on ability to attract and retain a high caliber of scientific staff and to provide an atmosphere that encourages imaginative, relevant research.

Interactions Between Universities and Governments

One of the comments cited in the previous section indicated concern over the inability of universities to provide training suitable to the needs of university graduates entering government establishments. There are several problems in this area. One is the general lack of experience in government work among university staff in the area of limnology and freshwater hydrobiology. This is now being met on a small scale through subvention programs that bring university staff members into the Services and Department for periods of 1–2 years. A second factor is that in thesis work students are trained to work on their own, cooperative effort with others being regarded as a form of "cheating." This contrasts with the situation in government research laboratories, where in complex problems that focus on science–society interfaces, the individual acts as a member of a team.

The latter question has received considerable discussion in recent years in terms of interdisciplinary training and the creation of institutes of environmental sciences. Interdisciplinary environmental institutes or centers are now functional in many Canadian universities: the University of British Columbia, University of Western Ontario, York University, University of Toronto, Université du Québec, Université Laval, and Dalhousie University, to mention but a few. For the most part they have been greeted with something less than enthusiasm by vested departmental interests in universities; and their performance has been of variable quality, particularly in the case of some water research centers that are still struggling or have died. DFE has supported a number of these developments; but it has never conducted an evaluation of the reasons for failure or success. In the case of one venture, the FRB support of work in the Department of Zoology at the University of Toronto in the early 1970s, the rise of aspirations coupled with early termination of support was cited by those involved as the primary reason for the subsequent breakup of the group involved.

Interactions of FWI and CCIW with universities in their immediate neighbourhoods are good. Provision has been made in the universities concerned for appointments to university staff permitting occasional lectures and direction of student theses. In the spring of 1976, 15 student theses were proceeding under the direction of CCIW staff members (7 M.Sc. and 8 Ph.D.) and 17 under the direction of FWI staff (10 M.Sc. and 7 Ph.D.).

One topic that has not received any serious attention is the possibility of nontraditional approaches to interdisciplinary training. I have argued the case (Vallentyne 1974) for cooperative theses in which students from different disciplinary backgrounds work together on an interdisciplinary thesis topic, on a joint pass–fail basis. The federal government could catalyze this by initiating a scholarship program, through the National Research Council, for students involved in such work. It is unlikely to get started without some such external support.

A number of persons interviewed in this study, and the Fisheries Research Board (1977), commented unfavorably on make-or-buy policy (Administrative Policy Branch, Treasury Board, 1977) in relation to university research. The intent of this policy is to shift federal expenditures to the industrial sector. Many members of the university community feel that they are being denied access to an area in which they have expertise to offer. Several comments were made on the inappropriateness of make-or-buy policy to research in the sense that most of the benefits of research, at least the development of expertise, arise from doing it. The mediation of contracts through the Department of Supplies and Services was viewed as inhibitory to the intermingling of government and nongovernment scientists, comparable to hiring a broker to make love. On the other hand, make-or-buy policy is applicable to monitoring and short-term investigations in areas where the onus of responsibility for the overall effort remains with the federal government.

It is difficult to place these comments on make-or-buy policy in perspective. Perhaps the only message is a need for broader statement of federal science policy that would encompass make-or-buy as only one of its components and would examine the desirability of a comparable policy statement in relation to university research. This question is connected with the need for a more sophisticated understanding of how practical innovations arise in science and technology, discussed in the first part of this report. Without such knowledge it is difficult to make any statement on the extent to which the implementation of make-or-buy policy may be jeopardizing national science.

Developing Citizen Support

The lack of comprehensive strategy is a major deterrent to effectiveness of DFE in meeting the objectives of its mandate. In the military, strategy centers on an analysis of constraints to meeting an objective. Strategy is, in effect, a plan to overcome the constraints. A comprehensive analysis of the constraints to attaining the objective of long-term environmental harmony between man and environment, including the built-in human constraints of instincts and habits, has to my knowledge never been made. As the more easily controllable forces of environmental degradation come under control (e.g.

municipal and industrial pollution) the need for behavior change will assume greater and greater importance.

There is one major constraint to achieving harmony between man and environment in which scientists in government and university have a capability that could be put to good use. This constraint is the human (biological) preoccupation with the immediate to the detriment of the long term. If there is one fundamental concept that permeates the soul of the scientist it is his recognition of the importance of the long term. Here is the question: Are there instruments of change that could put this motivation to work in focussing public attention on developing an attitude to the long term?

It can be argued that the scientist is ill suited to this task. In his essay on Milton, Macaulay (1825) made much of education as an obstacle to the poet:

"As civilization advances poetry almost necessarily declines . . . In proportion as men know more and think more they look less at individuals and more at classes. They therefore make better theories and worse poems. They give us vague phrases instead of images and personified qualities instead of men. They may be better able to analyse human nature than their predecessors. But analysis is not the business of the poet . . ."

All this is pertinent, but there is one crucial aspect to the communication problem that only the scientist can comprehend: its complexity. And that is why the scientist is the key to breaking through to nonspecialists. The public relations officer and the newspaper columnist may put things more simply and effectively, but they have no competence or credibility in dealing with this complexity, nor are they motivated with respect to the long term. A search among scientists might uncover some with talents that could focus public interest on the long term.

Although all forms of communication are pertinent in this connection, there may be a primary need for imaginative science writing on environmental issues in a way that first interests, and second informs. Books transcend time. The popularity of literature on science fiction shows that science is attractive to the public eye. But truth is stranger than fiction. It does not take much to see how the scientist might be portrayed in the role of a detective tracking down human manifestations of instinctive forces behind some of the killer chemicals at loose in society. As in "The French Connection" the real killer would always escape.

This is perhaps not likely to appeal to the bureaucratic mind; nevertheless, imaginative communication of this sort could be the key to the development of public attitude to the long term. B. F. Skinner's *Walden Two* (1948) is suggestive of a form that could be developed more effectively in focussing the public eye on complex long-term environmental problems. Many of H. G. Wells's writings were likewise motivated by a desire to transform society. There is a need for initiative in this area if we are to avoid the equally undesirable aspects of overmanaged or laissez-faire societies.

General Discussion

As noted above, concern over deterioration of the climate for research in Canada was (in 1976) neither peculiar to freshwater science nor to FMS or DFE. One indication of the extent of concern in Canada was reflected in the formation of a task force in 1976 under the Science Council of Canada to examine and report on the national climate for research (Task Force on Research in Canada 1977). The U.S. National Science Board (1976) showed with striking force and clarity that a comparable, if not greater, concern existed among leaders of science in the United States. I am not well informed on the situation in other countries; but, from conversations with colleagues in Europe, Japan, and the USSR, I would be surprised if the same situation did not apply there as well. In this section my intent is to show that certain aspects of the problem are universal, to examine the reasons why this is the case, and to suggest a general solution in the form of a scientific auditing function with an accent on natural resources to bring long-term considerations into sharper focus in decisions of the moment.

The concerns expressed to me in interviews stemmed from two fundamentally different sets of perceptions: the seeming *futility* of research because of the lack of attention, and sometimes even interest, of governments and the public in measures for the resolution of problems in the long term; and *frustrations* over undue interferences to the conduct and support of research. In conjunction, these suggest that the research community interviewed was primarily concerned with a perceived contraction of its ability to contribute to the resolution of problems in the long term. The research community was thus not solely concerned with the support and conduct of research; it was primarily concerned with the *usefulness* of its research. Research workers know instinctively that when long-term issues are neglected — as has been the case with environmental quality, resource depletion, and population growth — they always return in magnified, less easily controllable forms. The inevitable result is the appearance of a "time disruption syndrome" in the research community under the label of a deteriorating climate for research.

Although concern over time disruption predominated in the minds of the persons interviewed, there was a spatial aspect as well. This appeared in repeated references to the disruptive effect of involvement in "fire fighting" activities on the conduct of research. "Fire fighting" in the minds of scientists seems to conjure up a vision of hordes of people running about putting out fires one by one, without any serious attempt to develop systematized knowledge of causes and controls. In this sense, "fire fighting" is the antithesis of science.

Scientists recognize, often long before others, that "fires" exist, and they also know that "fires" have to

be put out. But they tend to view any investment of their time in "fire fighting," except under the most urgent conditions, as counterproductive, in that it detracts from their ability to contribute generalized solutions to the prevention and cure of fires. In the intervals between fires, senior managers accept this reasoning comfortably; but let one good fire show signs of going out of control and the detachment of scientists will instantly be viewed as irresponsible and even arrogant. At the same time, scientists will blame management for the fire because of neglect in developing the knowledge base necessary for controls and cures applicable over wide expanses of space and time. For these reasons, I believe that the roles of managers and scientists are best viewed as complementary (with some overlap) in space–time perspective, rather than as complementary in time perspective alone. There could hardly be a more fundamental philosophic distinction in employment roles.

The analysis and interpretation of this study is based on two central axioms: (1) space–time frame is the single most important characteristic differentiating the employment roles of managers and scientists; and (2) employment role is the primary determinant of the attitudes and behavior of individuals in organizations (Brown 1971). In plain words: managers are conditioned by their employment role to think and act "short" in regard to space and time, and scientists are conditioned by their employment role to think and act "long" in regard to space and time. If the attitudes and behavior of persons appointed to management and research roles are not preadapted to the space–time frame of thought and action demanded by the role, they will adjust to fit the role. Failure to make this adjustment inevitably results in frustration and incompetence (the common case), if not organizational or personal breakdown, accompanied by resignation or dismissal (the more visible, less common case). The consequences arising from this problem are similar in many respects to those arising from the separation of thought and action in our society (Ellul 1973, p. 27). In regard to the relationship between management and research, however, it is not that those who act do not think, and those who think do not act, but the conditioning of individuals by their employment roles to act and think with different perspectives in space and time.

I do not imply by this that there is no overlap of space–time frame in the roles of management and research or that all attitudes and behavior are determined by employment role. There is considerable flexibility in both respects. But, no one who has followed the changes in attitudes and behavior accompanying a change (or, more revealingly, interchange) of employment roles such as research and management, or labor and management, could question the importance of employment role in determining the attitudes and behavior of individuals in organizations. The expression, "shape up or ship out," summarizes this succinctly.

This division of labor in respect to space–time frame is not accidental; important benefits are derived from the separation that disappear in any attempt at fusion. The fundamental cause of problems arising from the separation of the two functions cannot be attributed to separation per se, as is sometimes naively supposed. The primary cause is a failure of cooperation, the sine qua non condition for operation of the principle of the division of labor. In characteristically human piecemeal fashion we have failed to appreciate that cooperation between management and research functions does not come about automatically; that it is to a large extent precluded by the very nature of the roles. We have failed to recognize that except for occasional intervals of harmony or truce, there always has been, and always will be, a deep philosophical conflict between management and research because of attitudes and behavior conditioned by differences in space–time perspective of the roles.

The part that suffers most in this relationship is research because of its subservience to senior management. Research tends to be subjected to the rules of management — despite the fact that many of those rules are better suited to the production line than to the research function. The attitudes and behavior of senior managers inevitably take precedence in shaping the direction of programs. New thoughts and new actions chase old thoughts and old actions from their minds to such an extent that they seem "flighty" to those whose eyes are focused on the long term. Senior managers in government or industry are apt to view short-term, localized problems and solutions as "real" and long-term, generalized solutions as "good in principle, but unworkable in practice." They are susceptible to the leaky roof syndrome, which says, "we don't need research," when times are good, and, "we can't afford research," when times are bad. They tend to view research as a commodity that can be bought and sold on the marketplace (e.g. the customer–contractor principle in the United Kingdom or make-or-buy policy in Canada when applied to research) rather than as a process in which the primary benefits arise from doing it. And they are prone to bet on the track (the mission or project) more than the horse (the person). On all these counts the senior manager, like the resource manager, is at odds with the research worker — not by desire, but by the nature of the role.

All of this will generally pertain despite the fact that "enlightened" senior managers appear on the scene from time to time and despite a premeditated flow of personnel from research into management functions. These factors and individual personalities mitigate, but do not fundamentally solve, the problem because the predominant cause of the problem stems from role-induced attitudes and behavior.

Quite apart from the above, there are four additional reasons why the research function tends to be neglected. In the first place, successful research findings are incorporated into management functions and the research area "rewarded" by reduced funding. Second, research

operates in an international level, yet requires justification nationally or subnationally for continued support. Third, to the politician and public it is an invisible process rather than a visible product that can be advertised and sold. Last, its promised rewards are distant in time, well beyond the usual political time frame.

The inescapable conclusion to all this is that, to ensure optimal representation of "long" space–time interests in decisions of the moment, the forces shaping the roles of senior managers must be changed. Senior managers must be made more accountable for "long" interests in space–time. The time is ripe for such a change in terms of emerging public recognition that many of our present problems stem from past inattention to long-term influences of environment, resources, and human population.

An evolution has in fact been taking place in this regard. During the past decade a number of self-appointed "auditors" of long-term public interest have appeared on the scene — pressure groups on pollution, consumers' rights, endangered species, population growth, conservation of resources, food additives, environmental contaminants, and the like. The common feature of these groups is that they act in the public interest without regard to monetary benefit. In addition to this, some governments have created ombudsman roles.

Collectively these "auditors" of the public interest have been effective in causing senior managers in government and industry to be more responsive to "long" interests in space–time; however, they lack an essential characteristic of the auditing function: full and complete access to the files and personnel of the organization under audit, with responsibility for public disclosure.

The diminishing supplies and increasing costs of natural resources provide fertile ground for emergence of an independent scientific auditing function available to governments and industries to give an accounting of wastage, inefficiency, and mismanagement of resources, with responsibilities extending into the long term and the need for self-correcting solutions. The prime value of such an independent function lies in the quality control it would impose on senior management in regard to resource utilization and in the improved image it would give to organizations in terms of public trust. It would not guarantee responsibility in the management of natural resources any more than financial auditing guarantees financial responsibility. The threat is exposure of poor management with consequent loss of face.

An independent resource auditing function could be instituted under, parallel to, or independently of, the existing financial auditing functions used by governments and industries. The choice should be based on which arrangement would yield the greatest credibility in terms of public confidence. Both governments and large resource industries are in need of improved credibility in regard to long-term issues. This need is likely to increase and transcend national boundaries as resources decline in quality, quantity, and dependability of supply.

Acknowledgments

I am first and foremost indebted to Dr A. E. Collin, who recognized the importance of the climate for research in the assignment he gave me to examine limnological research in Canada, and to the persons interviewed who gave so freely of their time. The latter are identified in the appendix. Secondly, I am indebted to the following persons who commented freely over a 2-day discussion period on substantive issues raised, and not raised, in the first draft of a paper on this topic: Dr A. L. Hamilton (then Director of Research and Resource Services, FWI), Dr M. G. Johnson (Director General, Ontario Region, FMS), Dr W. E. Johnson (then Director of the Pacific Biological Station, FMS), Dr K. Patalas (Senior Scientist, FWI), and Dr R. A. Vollenweider (Senior Scientist, CCIW). Finally, I am indebted to a number of persons who commented in detail on a later draft of this paper: Dr J. Barica, Dr J. W. Clayton, Dr R. D. Hamilton, Dr M. C. Healey, Mr K. E. Marshall, Dr D. Rosenberg, Dr R. Wagemann, and Dr R. Wallace, all of FMS; Mr J. P. Bruce and Dr R. K. Lane of EMS; Dr C. C. Lindsey, University of Manitoba; and Dr P. A. Larkin, University of British Columbia. Responsibility for content is mine alone.

References

ADMINISTRATIVE POLICY BRANCH, TREASURY BOARD. 1977. Policy and guidelines on contracting-out the government's requirements in science and technology. Supply and Services Canada, Ottawa, Catalogue No. BT32-10/1977: 23 p.

BEVERTON, R. J. H. 1974. Changes in the organization of government science in the United Kingdom. J. Fish. Res. Board Can. 31: 1275–1278.

BROWN, W. 1971. Organization. Heinemann Educational Books, London. 400 p.

CARTER, N. M. 1968. Index and list of titles, Fisheries Research Board of Canada and associated publications, 1900–1964. Bull. Fish. Res. Board Can. 164: 649 p.

1973. Index and list of titles, Fisheries Research Board of Canada and associated publications, 1965–1972. Fish. Res. Board Can. Misc. Spec. Publ. 18: 588 p.

COMROE, J. H., AND R. D. DRIPPS. 1976. Scientific basis for the support of biomedical science. Science 192: 105–111.

ELLUL, J. 1973. Propaganda. Vintage Books, Random House, New York, N.Y. xii + 320 p. (Transl. by Konrad Kellen and Jean Lerner)

ENVIRONMENTAL RESEARCH ASSESSMENT COMMITTEE. 1977. Research and development in the Environmental Protection Agency. A report to the U.S. Environmental Protection Agency from the Research Assessment Committee, Comm. Nat. Resour., Natl. Res. Counc. Natl. Acad. Sci. Vol. III: 105 p.

FISHERIES RESEARCH BOARD OF CANADA. 1977. Fisheries and aquatic sciences in Canada: an overview. J. Fish. Res. Board Can. 34: 710–727.

FREY, D. G. [ed.] 1963. Limnology in North America. Uni-

versity of Wisconsin Press, Madison, Milwaukee, and London, 734 p.

HAMILTON, R. D. 1976. Aquatic environmental quality — toxicology. J. Fish. Res. Board Can. 33: 2671–2688.

HARVEY, H. H. 1976. Aquatic environmental quality — problems and proposals. J. Fish. Res. Board Can. 33: 2634–2670.

JOHNSTONE, K. 1977. The aquatic explorers. A history of the Fisheries Research Board of Canada. University of Toronto Press, Toronto and Buffalo. 321 p.

LARKIN, P. A., AND W. J. D. STEPHEN. 1971. From formalin to Fortran: some facts and futures about basic biology in Canada. Background study for the Science Council of Canada. Spec. Study No. 18: 79 p.

MACAULAY, LORD. (1825). "Milton". *In* Selected essays and miscellaneous writings by Lord Macaulay. George Routledge and Sons, London and New York. 551 p.

NATIONAL SCIENCE BOARD. 1976. Science at the Bicentennial. A report from the research community. Government Printing Office, Washington, D.C. Stock No. 038-000-00280-5: 154 p.

NEEDLER, A. W. H. 1974. Reflections on the Fisheries Research Board. J. Fish. Res. Board Can. 31: 1283–1284.

POINCARÉ, H. 1914. Science and method. Dover Publications, Inc., New York, N.Y. 288 p. (Transl. from the original French edition of 1908 by Francis Maitland)

REGIER, H. A. 1976. Science for the scattered fisheries of the Canadian interior. J. Fish. Res. Board Can. 33: 1213–1232.

RICKER, W. E. 1975. Fisheries Research Board of Canada — Seventy-five years of achievements. J. Fish. Res. Board Can. 32: 1465–1490.

SENATE SPECIAL COMMITTEE ON SCIENCE POLICY (Chairman: The Honourable Maurice Lamontagne, P.C.). 1970, 1972, 1973. A science policy for Canada. Volume 1, A critical review: Past and present, 1970; Volume 2, Targets and strategies for the seventies, 1972; Volume 3, A government organization for the seventies, 1973. Supply and Services Canada, Ottawa.

SKINNER, B. F. 1948. Walden Two. The Macmillan Company, New York, N.Y. 320 p. (Macmillan Paperbacks Edition 1962)

TASK FORCE ON RESEARCH IN CANADA. 1977. Erosion of the research manpower base in Canada. The Science Council's Task Force on Research in Canada. Sci. Forum 10: 17–20.

VALLENTYNE, J. R. 1974. Limnology and education in the next decade. J. Fish. Res. Board Can. 31: 513–519.

Appendix

INSTITUTIONS VISITED AND PERSONS INTERVIEWED (EAST TO WEST)

Dalhousie University, Halifax: Dr M. Brilinsky, Mr Peter Brock, Dr L. M. Dickie, Dr F. R. Hayes, Mr Paul Keddy, Dr Patricia Lane, Dr K. H. Mann, Dr Ian McLaren, Dr J. G. Ogden, III.

Bedford Institute of Oceanography, Dartmouth: Dr R. J. Conover, Dr W. L. Ford, Dr Donald Gordon, Dr B. T. Hargrave, Dr C. R. Mann, Dr W. J. Sutcliffe.

Resource Branch (Halifax), Fisheries and Marine Service, Department of Fisheries and the Environment (letters only): Dr B. S. Muir, Dr W. Watt.

Biological Station, St. Andrews, Fisheries and Marine Service, Department of the Environment (letter only): Dr H. E. Welch.

Environmental Management Service (Halifax), Department of Fisheries and the Environment: Dr J. Kerekes.

Université Laval (Centreau), Québec: Dr C. Barbeau, Dr J. Llamas, Dr G. Moreau, Dr A. P. Plamondon, Dr A. Soucy, Dr J. L. Verrette.

Université du Québec, Institut National de la Recherche Scientifique-Eau, Ste Foy, Québec: Dr H. G. Jones, Dr H. St. Martin (former member), Mr M. Leclerc, Dr M. Ouellet, Dr L. Rousseau, Dr J. L. Sasseville, Dr S. A. Visser.

Service Environnement, Société d'Energie de la Baie James, Montreal: Dr A. Soucy.

British Petroleum, Canada, Montreal: Mr E. Howe.

McGill University, Montreal (telephone only): Dr F. H. Rigler.

Department of Fisheries and the Environment, Ottawa: Mr J. P. Bruce, Dr J. P. Cuerrier, DFE Steering Committee on Aquatic Environmental Quality.

Fish and Wildlife Research Branch, Ontario Ministry of Natural Resources, Maple, Ontario: Mr J. D. Roseborough.

University of Toronto, Toronto: Dr K. Hare, Dr H. H. Harvey, Dr H. Regier, Dr N. Solandt.

York University, Faculty of Environmental Studies, Toronto: Mr Paul Wilkinson, Miss A. Love.

Canada Centre for Inland Waters, Burlington: Dr J. M. Cooley, Dr M. Dick, Dr F. Elder, Mrs E. A. C. Fosdick, Dr W. Glooshenko, Dr P. Hamlin, Dr P. V. Hodson, Dr M. G. Johnson, Dr J. R. M. Kelso, Dr A. R. LeFeuvre, Dr T. Nelson, Dr G. K. Rodgers, Miss Peggy Sinclair, Dr Peter Sly, Dr R. L. Thomas, Dr R. A. Vollenweider, Dr N. Watson.

Freshwater Institute, Winnipeg: Mr F. A. J. Armstrong, Dr J. Barica, Dr D. M. Cauvin, Dr L. C. Dugal, Dr W. Faulkner, Dr T. Hara, Dr A. L. Hamilton, Dr R. D. Hamilton, Dr T. Jackson, Dr G. H. Lawler, Dr S. Lawrence, Mr E. Marshall, Dr R. Newbury, Dr K. Patalas, Dr O. Sæther, Dr D. W. Schindler, Dr D. P. Scott.

University of Manitoba, Winnipeg: Dr C. C. Lindsey, Dr F. J. Ward.

University of Saskatchewan, Saskatoon: Dr U. T. Hammer.

Saskatchewan Fisheries Laboratory, Saskatoon: Dr F. M. Atton.

Saskatchewan Research Council, Saskatoon: Dr B. H. Gunn, Dr T. P. Pepper, Dr W. Sawchyn.

University of Alberta, Edmonton: Dr R. C. von Borstel, Dr. H. F. Clifford, Dr J. S. Nelson, Dr J. R. Nursall, Dr R. E. Peter, Dr A. L. Steiner.

Research Secretariat, Alberta Department of the Environment, Edmonton: Dr B. Hammond, Dr S. B. Smith.

University of British Columbia, Vancouver: Dr C. S. Holling, Dr Peter Larkin, Dr Janet Stein.

Environmental Management Service, Department of Fisheries and the Environment, Vancouver: Mr M. Clarke.

B.C. Research Council, Vancouver: Dr Terry Howard, Dr Paul Trussell.

Pacific Environment Institute, West Vancouver: Dr Ralph Daley, Dr G. L. Greer, Dr C. D. Levings, Dr I. H. Rogers, Dr J. S. Stockner, Dr M. Waldichuck.

Water Pollution Branch, British Columbia (Vancouver and Victoria): Dr R. J. Buchanan, Miss I. Kalnins, Mr J. Leach.

Pacific Biological Station, Nanaimo: Dr R. J. Beamish, Dr J. R. Brett, Dr M. C. Healey, Dr W. E. Johnson, Dr Z. Kabata, Mr Robin J. LeBrasseur, Dr Leo Margolis, Mr J. McDonald, Dr J. H. Mundie.

International Great Lakes Association Meeting, Guelph: Dr Graham Daborn, Dr H. B. N. Hynes, Dr James Kramer, Dr C. H. Mortimer, Dr Gian Vascotto.

Consultant Industries: Dr Shirley Conover, Dr Ian Dickson, Dr R. J. Jackimchuk, Mr Dmitri Stone.

OBITUARY

Otto Christian Young

1899-1977

Otto Christian Young died in West Vancouver, British Columbia, on October 16, 1977, after a brief illness in his 78th year.

An employee of the Fisheries Research Board of Canada for 34 years, Otto Young gained an international reputation for his researches on the physics of refrigeration as applied to the maintenance of high quality during the handling, holding, and transportation of chilled or frozen fish. His enthusiasm in his researches encouraged his co-workers and assistants. He could persuade fishermen, fishing companies, also transportation agencies, to loan or construct equipment which he could modify for testing his recommendations in practice. His outstanding personality, honesty, and integrity impressed all with whom he worked.

He was born in Stratford, Ontario. While living in Wakaw, Saskatchewan, he decided to further his physics and mathematics education, but was 30 miles from the nearest collegiate and 60 miles from the University of Saskatchewan in Saskatoon. Consequently he had to study by correspondence for his university entrance. Finances were a problem, so he took a teachers training course in Saskatoon and taught for 3 years. On gaining entrance to the university in Saskatoon in the fall of 1923 he soon received an instructorship at the university to aid his finances until he graduated in 1927 with a B.Sc. Two years later he obtained his master's degree in engineering; for his thesis he worked on the reclamation of automobile crankcase oil and was able to recover a product of suitable quality except that it lacked the greenish fluorescence of fresh oil. This thesis was conducted under Professor I. M. Fraser, who later became the University of Saskatchewan representative on the Fisheries Research Board of Canada for some years.

Through Professor Fraser Otto learned of a forthcoming opening for a research engineer under Dr D. B. Finn, then director at the Prince Rupert, British Columbia, station of the Fisheries Research Board of Canada. Otto successfully applied for the position and moved to Prince Rupert with his bride Ione in 1929. An additional building for the station was under consideration at the time of his arrival, so for a while he was engaged in developing plans and specifications for this addition and being supervising engineer during its construction.

Otto's first research project in the new building was studying means of reducing dehydration of frozen fish in cold storage rooms by reducing the temperature differential between the fish and the refrigerating coils. This led to his development of "jacketed" cold storage rooms and experiments with noncracking glazes for fish stored in them. He then commenced studies of the effects of rate and temperature of freezing on the texture and delectability of frozen fish. Microscope examination of the growth of ice crystals within and between the cells of the freezing fish showed that the more rapid the freezing, the less "drip" ensued on thawing for cooking. To test the results of his different rates of freezing and temperatures of storage, he trained a tasting panel including a cross section of Prince Rupert residents, who were supplied with unidentified samples for reporting on the edible acceptability of the cooked fillets or steaks. Their results helped to dispel the opinion held by many Canadian consumers that if fish had to be frozen for long-distance transportation, its quality would be impaired.

Otto believed that most of the misconception about the edible quality of frozen fish, particularly halibut, transported to distant markets in the then existing type of Canadian railway refrigerator cars arose from the way the refrigeration was applied in the car. Com-

Printed in Canada (J5034)
Imprimé au Canada (J5034)

mencing in 1953 he built several large-scale models at the Prince Rupert Station to test other ways of situating the refrigerating medium and later induced the Canadian National Railway to loan a car which he modified to have the refrigerating ice-and-salt mixture in tanks under the roof of the car instead of in upright bunkers inside the ends of the cars. The results during transcontinental shipments of frozen halibut in the modified car accompanied by Otto and his electrical recording thermometers in an adjoining car were so encouraging that after the Station was moved to Vancouver in 1942 he persuaded the railways to let him test the feasibility of installing a diesel-operated "packaged" refrigerating unit and refrigerator coils to replace ice-and-salt refrigeration. An American company designed a suitable unit and during tests lasting until 1950 Otto made further trips across Canada to observe the temperatures within the fish and the car and arranged tasting panels to judge the acceptability of the fish at its destination. The railway companies began to adopt the use of a mechanically refrigerated unit because it could be made to serve the dual purpose of either keeping frozen fish frozen during summer trips, or by "running the unit backwards" it would provide heat to keep other type of loads from freezing during winter trips. However, about that time railway transportation of fish began to be supplanted by trucks having mechanical refrigeration.

Although Otto's research work at the Station concentrated on refrigeration engineering from 1929 to 1950, he collaborated with other staff members in various studies such as designing a large metal sampling device for determining the bacterial content of seawater; use of ultraviolet light for sterilizing brines used in processing fish products; improvements in canning, smoking, drying, and dehydrating procedures and equipment; modification of fishing vessel holds, etc. For his contributions to the above fields of research Otto was awarded the honor of being made a Member of the Order of the British Empire (M.B.E.) in 1946. In 1948 he spent a short time in Shanghai, China, as an advisor at the request of the United Nations. He was author or coauthor of 57 scientific and interpretative articles and contributed the 21-page chapter "Transportation of Fishery Products" in the second edition (1951) of the widely recognized work *Marine Products of Commerce*. He was also a member of the Society of Professional Engineers.

Otto's achievements and knowledgeability led to his being transferred in July 1950 to the Board's Headquarters Unit in Ottawa to assume administrative duties first as Scientific Assistant to the Chairman, and later as Assistant Chairman, in matters relating to the Board's fisheries technological fields. He held the latter position until his retirement to West Vancouver in 1963. During 1958 he was seconded for several months under the Colombo Plan to Ceylon for organizing and demonstrating modern fisheries facilities there. In 1963 after his retirement he spent 6 months in Newfoundland advising on similar facilities.

In addition to his scientific career Otto was a member of a church choir, and enthusiastically participated in tennis, badminton, bowling, and golfing. He is survived by his wife Ione, two sisters, a daughter (Mrs. Bruce Carter) of West Vancouver, a son Donald of Montreal, and seven grandchildren.

NEAL M. CARTER

Ichthyology. *2nd ed. Karl F. Lagler, John E. Bardach, Robert R. Miller, and Dora R. May Passino. John Wiley and Sons, Inc., New York, N.Y., 1977. xviii + 506 p. $18.95.*

The second edition of *Ichthyology* is a most welcome reference text. During the close to 15 years since the first edition was published, there has been a significant expansion of scientific studies on fishes. There have been no up-to-date, in-depth reference books for beginning ichthyologists, despite the appearance of many advanced and specialized monographs on fish biology.

In *Ichthyology* the student is exposed to the basic anatomy, physiology, biochemistry, ecology, behavior, taxonomy, and evolution of fishes, presented by a team of experts well known for their research on these topics. This broad approach to the study of fishes enables the untrained student to explore the subject despite a varied background.

This particular reviewer is especially interested in the treatment of the neural and sensory systems (Chapter 11, Integration). These sections are well handled and are written in an interesting style, but they are somewhat unbalanced in that they are either too superficial in view of their importance, or too specialized without detailed explanations for the beginning student. For example, there is an added section on the function of the forebrain of rayfin fishes. In this section mention is made of the pallial and subpallial areas, and some details are given of nerve tracts through these regions. But this material is highly specialized and will be difficult for the beginner to understand. If these new text sections were supplemented by new text-figures, their clarity would have been enhanced. Somewhat similar comments can be made for Table 11.1 in this same chapter. The table contains no supplementary material from the previous edition, but it would be a more useful table if some corresponding figures were added to help the student untrained in vertebrate neuroanatomy. The section dealing with intelligence and behavior in the chapter "Integration" has been expanded, and this new material is a timely addition in view of the importance that fish behavior studies have, relevant to pollution and the environment. But this section is so full of interesting material that some of it gets lost because of its compactness; a breakdown into various subsections would have helped. The parts on sense organs were good in the first edition, and remain so, with much of the material brought up-to-date.

While the generalist approach to fishes is useful for the beginner, it sometimes fails in that it doesn't provide sufficient awareness of the many unknowns in need of study and exploration, for example the treatment of the fish pineal. The approach is dated and in this form of presentation will not be likely to stimulate much research interest. On page 317, the pineal is depicted as one in which "no distinct function has been unequivocally demonstrated," but two categories of hypotheses include "one emphasizing primarily a sensory role and the other a secretory function." This starts out in a rather exciting fashion, but falls short when the generalizations given are as brief as for the sensory role, "the pineal body is a photosensory structure; it acts as a baro- or chemoreceptor for cerebrospinal fluid; or it functions as a mediator in the olfactory response to exohormones."

Ichthyology is a valuable text for upper-level undergraduate students and first-year graduate classes. In association with the many expanded sections in this new edition, many new references have been added. It is impossible for a book as basic as this is to cover all of the recent relevant references. The references are adequate, but for some topics, such as the inner ear and the lateral line, topics in which the reviewer is especially well informed, it would have been helpful to include some of the excellent recent review articles written in the English language, in addition to or instead of the classical older reviews which require translation.

This textbook on fishes will be used widely in academic and industrial applications. It's accurate and thorough coverage of fish biology makes it a valuable title for reference collections in the aquatic sciences.

PHYLLIS H. CAHN

C. W. Post Center
Department of Marine and Environmental Science
Long Island University
Greenvale, N.Y. 11548, USA

(R172)

Biological Monitoring of Water and Effluent Quality. *Edited by John Cairns Jr., K. L. Dickson, and G. F. Westlake. American Society for Testing and Materials, Philadelphia, Pa., 1976. vii + 246 p. $24.25.*

It is not obvious from the book whether the stated aims of the symposium, at which the papers in this book were presented, were achieved. Certainly the book provides an overview of the state of the art of biological monitoring and provides justification for the use of such monitoring, but the reliability, acceptance, and cost of the methods are never discussed in detail.

Biological monitoring is needed to evaluate effluent and water quality because information or legislation based solely on physical and chemical parameters may not protect the local aquatic environment from the adverse effects of pollutants or may, by legislation being overly stringent, place an unnecessary economic burden on industry. Biological monitoring can evaluate changes in effluent quality and, if feedback from the system is rapid, enable undesirable changes in effluent quality to be corrected before the effluent is discharged. Biological monitoring can assess the biological state of the water body and determine whether environmental deterioration is occurring. Such monitoring of effluent and water quality can be used as part of pollution control or environmental protection legislation.

The majority of papers in the book describe *techniques* for biological monitoring. The papers on continuous monitoring provide a better overview of that topic than do the papers on monitoring to assess the biological state of water bodies. Most techniques for the continuous monitoring of effluent quality utilized the respiratory or locomotory behavior of fish, but Paparo and Sparks recommended utilizing the ciliary beating of excised clam gills. Monitoring of some responses has been automated and linked to alarm systems

which alert operators if the response changes. An automated biological monitoring system utilized the respiration rate of bluegills (*Lepomis macrochirus*) to monitor effluent quality of an industrial plant (Westlake and van der Schalie), and the rheotactic behavior of rainbow trout (*Salmo gairdneri*) was utilized to monitor the quality of the river Rhine in a pilot plant study (Poels). Morgan's automated system for monitoring opercular rhythms of fish only triggered an alarm when opercular rhythm increased, but Westlake and van der Schalie showed that chlorine caused an actual or apparent decrease in the frequency of opercular rhythm. Ladd questioned whether research into biological monitoring of effluent quality was worthwhile since the goal for water pollution control in the USA is zero discharge of effluent.

The papers on biological monitoring of water quality are concerned with determining whether biological communities change with time. Livingston pointed out some complexities caused by temporal variation which must be considered in designing adequate monitoring programs. Most papers pointed out that biological monitoring usually will not identify causes of biological changes, but well-designed biological monitoring programs can detect the effects of dams, organic pollution, toxicants, and improved waste treatment on several biological communities (Patrick), and changes in nutrient and organic waste loadings can be detected by monitoring community production and respiration (Kelly et al.). Green discussed the right and wrong ways of analyzing biological data to determine whether a specific environmental change affected a biological community.

The discussion of criteria for biological monitoring by Poels and by Cairns, and the discussions of the future needs for biological monitoring related more to biological monitoring of effluent quality than to the monitoring of water quality. Both Doudoroff and Mount identified the need to develop suitable bioassays for biological monitoring, whose results would predict actual harmful effects in the aquatic environment or maximum harmless concentrations.

The book provides a useful summary of the 1975 status of biological monitoring, especially of effluents, but much information in the book is not new. People involved with water pollution control and environmental protection or with bioassay development should be aware of the contents of the book, especially the keynote address by Doudoroff and the summary by Cairns.

R. McV. CLARKE

Department of Fisheries and the Environment
Fisheries and Marine Service
Freshwater Institute
Winnipeg, Man. R3T 2N6

(R169)

Impact of Acid Precipitation on Forest and Freshwater Ecosystems in Norway. Research Report 6/76. *Edited by Finn H. Braekke. Norwegian Council for Scientific and Industrial Research, Agricultural Research Council of Norway, and Norwegian Ministry of Environment, 1976. 111 p.*

We are only beginning to appreciate the impact that atmospheric fallout has on ecosystems. A component of this fallout is acidic and in some regions acidic fallout has serious detrimental effects, especially on lakes. Norway probably has suffered more from acidic fallout than any other country and it is appropriate that in recent years a significant effort has been concentrated on determining the damage caused by acid fallout to the fauna and flora of forests and lakes. In 1973 an interdisciplinary research group was formed in Norway (the SNSF project or Acid Precipitation — Effects on Forest and Fish) to establish as precisely as possible the effects of acid precipitation, and other pollutants when relevant to acid precipitation, on forests and freshwater fishes.

The results of the first phase of the study up to 1975 have been summarized in the report *Impact of Acid Precipitation on Forest and Freshwater Ecosystems in Norway*. A second phase of research is scheduled to last until 1979, when it is planned that a more comprehensive summary will be published. This report therefore is an interim report. Many of the projects are still in progress and some results must be considered to be preliminary. Nevertheless, there is merit in summarizing the information collected to date, and the data, the interpretations, the many references to Norwegian reports, and the style of presentation will be useful to those actively involved in acid-precipitation research as well as being comprehensible to those requiring a more general appreciation of such problems.

The report is divided into five sections. There is a general introduction and synthesis followed by four parts: the deposition of air pollutants, the effects of acid precipitation on coniferous forests, the effects of acid precipitation on freshwater chemistry, and the effects of acid precipitation on freshwater organisms.

Section 2 supplies convincing data, some of which is confirmatory, that depositions of sulphur compounds and other pollutants occur in both dry and wet deposition and that a major portion of these pollutants originates from areas in Great Britain and continental Europe. Much of this fallout was found to be deposited during very short periods. For example, in one area 25% of the excess sulphate was deposited in 15 days during the 3-year period 1972–75. Changes in the acidity of precipitation were most pronounced from 1955 to 1965. Unfortunately, no explanation is offered to account for the apparent change in rate of acidification beginning in 1965. This section also has a recurring esoteric reference to "the model." Again it is unfortunate that no details of this apparently important analysis were included.

Section 3 indicates that increased foliar leaching of nutrients can occur with increased rain acidity as well as some loss of nutrients from some soils. However, no information was obtained that suggested that acid precipitation was reducing forest production in Norway. Decomposition of soils or germination of seedlings were not seriously affected by average concentrations of acid found in precipitation. In fact, in one experiment an increase in tree growth was correlated with increasing acidity of precipitation.

Acid precipitation has its most profound effects on aquatic ecosystems. Rivers and smaller lakes that are poorly buffered as a consequence of thin soil layers and bedrock poor in calcium and magnesium minerals are extremely sensitive to acid inputs. Section 4 documents the major anion change in lakes from bicarbonate to sulphate, associated with an increase in concentrations of H^+, SO_4^{2-}, and Al^{3+}. Associated with this change in lakes is a loss in the watershed of Ca^{2+}, Mg^{2+}, and Al^{3+}, and a retention of H^+, NO_3^-, and NH_4^+. The suggestion that the washout of cations from the watershed may affect forest productivity is inconsistent with the conclusion of the previous section that no loss of productivity could be demonstrated. No mention is made of the high concentra-

tions of manganese and zinc that have been reported for North American acidified lakes.

Acidification of waters resulted in a reduction in the diversity of phytoplankton and invertebrate communities. Decomposition of organic material is inhibited and certain types of algae accumulate. The most spectacular effect has been with the loss of fish. It is estimated that fish populations from 20% of the waters in southern Norway have been affected by increasing acidity. Of particular importance has been the loss of salmonids. The disappearance of these fishes results from kills of adult fish and egg and fry mortalities. Physiological studies showed that fishes in waters with higher ion content may be better protected against sudden pH decreases.

It is unnecessary to review the substance of this report extensively. It is a preliminary report and is so stated to be. The real assessment of this report, and the project as a whole, will come when the final overview of the effects of acid fallout on forests and lakes in Norway is published.

R. J. BEAMISH

Department of Fisheries and the Environment
Fisheries and Marine Service
Pacific Biological Station
Nanaimo, B.C. V9R 5K6 (R171)

Editor's note:

It is not usual to have a review of an interim report prepared; however, acid precipitation is a serious problem in many mining and refining areas of Canada. Hence, the report on the Norwegian experience, even if incomplete, is extremely important. It was my good fortune to be able to persuade Dr Beamish to undertake the review, since he is one of Canada's foremost authorities on the subject.

D. P. SCOTT
Book Review Editor

Books Received/Livres reçus

October 1977

Coelenterate Ecology and Behaviour. *Edited by G. O. Mackie. Plenum Publishing Corporation, New York, N.Y., 1976. xiv + 744 p. $49.50.* (This volume consists of 73 selected papers from the Third International Symposium on Coelenterate Biology, held in Victoria, B.C. in May, 1976.)

The Coastline. *Edited by R. S. K. Barnes. John Wiley and Sons, Inc., Somerset, N.J., 1977. xii + 356 p. $28.50.* (A multidisciplinary, predominantly British approach to the ecology of marine coastlines.)

COMING NEXT MONTH/À PARAÎTRE LE MOIS PROCHAIN

pH-induced changes in blood lead of lead-exposed rainbow trout (*Salmo gairdneri*)
P. V. Hodson, B. R. Blunt, and D. J. Spry

Effect of graded levels of supplemental ascorbic acid in practical diets fed to rainbow trout (*Salmo gairdneri*) **J. W. Hilton, C. Y. Cho, and S. J. Slinger**

Isotopic composition of dissolved inorganic carbon in the Great Lakes **R. R. Weiler and J. O. Nriagu**

Pathogenic vibrios in confinement-reared and feral fishes of the Maine–New Hampshire coast
R. G. Strout, E. S. Sawyer, and B. A. Coutermarsh

A simple model for cross-shelf mixing on the Scotian Shelf
R. W. Houghton, P. C. Smith, and R. O. Fournier

Paralytic toxins in the dinoflagellate *Gonyaulax excavata* and in shellfish
A. W. White and L. Maranda

Tissue uptake, subcellular distribution, and metabolism of $^{14}CH_3HgCl$ and $CH_3{}^{203}HgCl$ by rainbow trout, *Salmo gairdneri* **K. R. Olson, K. S. Squibb, and R. J. Cousins**

Comparative recoveries of planted yearling and fall fingerling brook trout (*Salvelinus fontinalis*) from Ontario lakes **J. M. Fraser**

Polarographic studies on the nature of cadmium in scallop, oyster, and lobster
C. L. Chou, J. F. Uthe, and E. G. Zook

Notes

Fish cell culture: properties of a cell line from the sheepshead, *Archosargus probatocephalus*
W. M. Law, R. D. Ellender, J. H. Wharton, and B. L. Middlebrooks

Chill stowage and development of rancidity in frozen Pacific herring, *Clupea harengus harengus*
E. Bilinski, R. E. E. Jonas, and Y. C. Lau

Technique pour la comparaison des échanges branchiaux de Cl^- en eau douce chez *Salmo gairdneri* in vivo et in vitro sur la tête isolée perfusée **P. Payan, P. Pic, and G. de Renzis**

Toxicity of a mixture of metals on freshwater algae **P. T. S. Wong, Y. K. Chau, and P. L. Luxon**

RECENT PUBLICATIONS / RÉCENTES PUBLICATIONS

The number following each title in each series refers to the establishments listed at the end of the section.

Les nombres qui suivent les titres de chacune des séries désignent les établissements suivants à la fin de la section.

Recent Studies

Until 1970, reprints of these articles had been included in an annual volume of "Studies," composed of two parts. The final binding was the 1969 Studies, Part 2, which included No. 1355. These are no longer bound and distributed. We continue, however, to number and list all articles on investigations published in other periodicals, which henceforth may be obtained in reprint form only from the author or originating establishment.

Récentes études

Jusqu'en 1970, ces articles étaient réimprimés, puis reliés dans un volume annuel d'études, comprenant deux parties. Les études de 1969, partie 2, incluant le n°1355, ont été les dernières à être reliées. Nous n'en faisons désormais plus la reliure ni la distribution. Nous continuons cependant de numéroter les articles et d'en établir des listes d'études sur des recherches mentionnées dans d'autres périodiques. On peut donc se les procurer, sous leur forme réimprimée seulement, de l'auteur ou du service dépositaire.

2414. Beames, R. M., R. M. Tait, J. N. C. Whyte, and J. R. Englar. 1977. Nutrient utilization experiments with growing pigs fed diets containing from 0 to 20% kelp (*Nereocystis Luetkeana*) meal. Can. J. Anim. Sci. 57: 121–129. (2)

2415. Sieliwanowicz, B., M. Yamamoto, L. Stasiuk, and M. Laskowski Sr. 1975. Studies of specificity of deoxyribonuclease from salmon testes. Biochemistry 14: 39–46. (2)

2416. Reinke, J., J. F. Uthe, H. C. Freeman, and J. R. Johnston. 1975. The determination of arsenite and arsenate ions in fish and shellfish by selective extraction and polarography. Environ. Lett. 8: 371–380. (8)

2417. McLeese, D. W., R. L. Spraggins, A. K. Bose, and B. N. Pramanik. 1977. Chemical and behavioral studies of the attractant of the lobster (*Homarus americanus*). Mar. Behav. Physiol. 4: 219–232. (6)

2418. Kabata, Z., and E. A. Koryakov. 1974. Morphological variability of (*Salmincola cottidarum*) Messjatzeff, 1926 (*Copepoda: Lernaeopodae*), a parasite of the Baikal cottids. Parazitologiya 8: 306–311. (1)

2419. MacFarlane, L. R. 1976. Automatic feeder for delivery of high-fat starter food to swim-up fry of Atlantic salmon. Prog. Fish Cult. 38: 106–107. (6)

2420. Messieh, S. N. 1975. Growth of the otoliths of young herring in the Bay of Fundy. Trans. Am. Fish. Soc. 104: 770–772. (6)

2421. Stasko, A. B., R. M. Horrall, and A. D. Hasler. 1976. Coastal movements of adult Fraser river sockeye salmon (*Oncorhynchus nerka*) observed by ultrasonic tracking. Trans. Am. Fish. Soc. 105: 64–71. (6)

2422. Stasko, A. B. 1975. Progress of migrating Atlantic salmon (*Salmo salar*) along an estuary, observed by ultrasonic tracking. J. Fish. Biol. 7: 329–338. (6)

2423. Stevens, E.D., and A. M. Sutterlin. 1976. Heat transfer between fish and ambient water. J. Exp. Biol. 65: 131–145. (6)

2424. Sutterlin, A. M. 1974. Pollutants and the chemical senses of aquatic animals — perspective and review. J. Chem. Senses Flavor. 1: 167–178. (6)

2425. Mulkins-Phillips, G. J., and J. E. Stewart. 1974. Effect of environmental parameters on bacterial degradation of bunker C oil, crude oils, and hydrocarbons. Appl. Microbiol. 28: 915–922. (6)

2426. Margolis, L., F. Moravec, and T. E. McDonald. 1975. *Rhabdochona kisutchi* sp. nov. (Nematoda: Spiruroidae) from coho salmon, *Oncorhynchus kisutch* (Walbaum), of western Canada. Can. J. Zool. 53: 960–966. (1)

2427. Razzell, W. E. 1975. Aldehyde dehydrogenase from *Pseudo monas aeruginosa*. Methods Enzymol. 41: 348–354. (2)

2428. Ackman, R. G. 1977. Rapeseed oil: Chemical and physical characteristics. Bull. Rapeseed Assoc. Can. (8)

2429. Ackman, R. G., C. A. Eaton, J. C. Sipos, F. M. Loew, and D. Hancock. 1977. A comparison of fatty acids from high levels of docosenoic acids of rapeseed oil (Erucic acid) and of partially hydrogenated fish oil (primarily cetoleic acid) in a non-human primate species in a short-term exploratory study. Bibl. Nutr. Dieta 25: 170–185. (8)

2430. Wells, P. G., and P. D. Keizer. 1975. Effectiveness and toxicity of an oil dispersant in large outdoor salt water tanks. Mar. Pollut. Bull. 6: 153–157. (7)

2431. Landymore, A. F., and N. J. Antia. 1977. Growth of a marine diatom and a haptophycean alga on phenylalanine or tyrosine serving as sole nitrogen source. J. Phycol. 13: 231–238. (3)

2432. Kabata, Z. 1977. Redescription of *Salmincola longimanus* Gundrizer, 1974 (Copepoda: Lernaeopodidae). Proc. Biol. Soc. Wash. 90: 189–193. (1)

2433. Parker, R. R., and J. Sibert. 1976. Responses of phytoplankton to renewed solar radiation in a stratified inlet. Water Res. 10: 123–128. (1)

2434. Thompson, J. A. J., J. C. Davis, and R. E. Drew. 1976. Toxicity, uptake and survey studies of boron in the marine environment. Water Res. 10: 869–875. (3)

2435. SYMONS, P. E. K. 1977. Dispersal and toxicology of the insecticide fenitrothion; predicting hazards of forest spraying. Residue Rev. 68: 1–36 (6)
2436. TAGUCHI, S., AND T. PLATT. 1977. Assimilation of $^{11}CO_2$ in the dark compared to phytoplankton production in a small coastal inlet. Estuarine Coastal Mar. Sci. 5: 679–684. (7)
2437. MAHOOD, H. W., AND I. H. ROGERS. 1975. Separation of resin acids from fatty acids in relation to environmental studies. J. Chromatogr. 109: 281–286. (3)
2438. ROGERS, I. H., J. C. DAVIS, G. M. KRUZYNSKI, H. W. MAHOOD, J. A. SERVIZI, AND R. W. GORDON. 1975. Fish toxicants in kraft effluents. Tappi 58: 136–140. (3)
2439. MARGOLIS, L., AND M. BEVERLEY-BURTON. 1977. Response of mink (*Mustela vison*) to larval *Anisakis simplex* (Nematoda: Ascaridida). Int. J. Parasitol. 7: 269–273. (1)
2440. SUBBA RAO, D. V. 1975. *Planktoniella sol* (Wallich) Schutt (Bacillariophyceae, Coscinodiscaceae), a new record for north-western Atlantic coastal waters. Phycologia 14: 183–185. (7)
2441. SCOTT, K. R., AND K. I. HAYAKAWA. 1977. Simplified prediction of freezing and thawing times of foods. ASHRAE Trans. 83: 541–548. (4)
2442. ZITKO, V., AND W. G. CARSON. 1977. Uptake and excretion of chlorinated diphenyl ethers and brominated toluenes by fish. Chemosphere 6: 293–301. (6)
2443. MACCAULL, W., AND T. PLATT. 1977. Diel variations in the photosynthetic parameters of coastal marine phytoplankton. Limnol. Oceanogr. 22: 723–731. (7)
2444. PINHORN, A. T. 1976. Catch and effort relationships of the groundfish resource in ICNAF subareas 2 and 3. Int. Comm. Northwest Atl. Fish. Sel. Pap. 1: 107–115. (9)
2445. PENROSE, W. R., AND W. R. SQUIRES. 1976. Two devices for removing supersaturating gases in aquarium systems. Trans. Am. Fish. Soc. 105: 116–118. (9)
2446. PENROSE, W. R. 1974. Arsenic in the marine and aquatic environments: Analysis, occurrence, and significance. CRC Crit. Rev. Environ. Contr. 4: 465–482. (9)
2447. PENROSE, W. R., H. B. S. CONACHER, R. BLACK, J. C. MÉRANGER, W. MILES, H. M. CUNNINGHAM, AND W. R. SQUIRES. 1977. Implications of inorganic/organic interconversion on fluxes of arsenic in marine food webs. Environ. Health Perspect. 19: 53–59. (9)
2448. PAYNE, J. F. 1976. Field evaluation of benzopyrene hydroxylase induction as a monitor for marine petroleum pollution. Science 191: 945–946. (9)
2449. SHAW, D. H., R. L. GARE, AND M. A. KENNEDY. 1977. Chemical and sensory changes during storage of witch flounder (*Glyptocephalus cynoglossus*) in ice. J. Food Sci. 42: 159–162. (9)
2450. PAYNE, J. F., AND W. R. PENROSE. 1975. Induction of aryl hydrocarbon (Benzo (a) pyrene) hydroxylase in fish by petroleum. Bull. Contam. Toxicol. 14: 112–116. (9)
2451. SIMS, G. G., W. E. ANDERSON, AND S. VARGA. 1977. Measurement and significance of soft undesirable solids in minced lobster meat. J. Inst. Can. Sci. Technol. Aliment. 10: 191–196. (8)
2452. STOCKNER, J. G. 1975. Phytoplankton heterogeneity and paleolimnology of Babine lake, British Columbia, Canada. Verh. Int. Ver. Limnol. 19: 2236–2250. (3)
2453. THOMPSON, J. A. J. 1975. Copper in marine waters — effect of mining wastes, p. 273–284. *In* Int. Conf. on Heavy Metals in the Environment, Toronto, Ont., October 1975. (3)
2454. OLAFSON, R. W., AND J. A. J. THOMPSON. 1974. Isolation of heavy metal binding proteins from marine vertebrates. Mar. Biol. 28: 83–86. (3)
2455. KICENIUK, J. W., AND D. R. JONES. 1977. The oxygen transport system in trout (*Salmo gairdneri*) during sustained exercise. J. Exp. Biol. 69: 247–260. (9)
2456. PLATT, T., D. V. SUBBA RAO, AND K. L. DENMAN. 1977. Quantitative stimulation of phytoplankton productivity by deep water admixture in a coastal inlet. Estuarine Coastal Mar. Sci. 5: 567–573. (7)
2457. ANDERSON, R., M. KATES, M. J. BAEDECKER, I. R. KAPLAN, AND R. G. ACKMAN. 1977. The stereoisomeric composition of phytanyl chains in lipids of Dead Sea sediments. Geochim. Cosmochim. Acta 41: 1381–1390. (8)

Technical Report Series

Technical Reports are research documents that are of sufficient importance to be preserved, but which for some reason are not appropriate for primary scientific publication. Inquiries concerning any particular Report should be directed to the issuing establishment.

681. HARE, G. M. 1977. Atlas of the major Atlantic coast fish and invertebrate resources adjacent to the Canada–United States boundary areas. Fish. Mar. Serv. Res. Dev. Tech. Rep. 681: 97 p. (6)
682. TSUYUKI, H., J. CHENG, S. N. WILLISCROFT, A. P. RONALD, AND L. HUZYK. 1976. Pacific salmon roe processing. Fish. Mar. Serv. Res. Dev. Tech. Rep. 682: 39 p. (2)
683. BRUCE, W. J., AND R. F. PARSONS. 1976. Age, growth and maturity of lake chub *Couesius plumbeus* in Mile 66 brook, Ten Mile lake, western Labrador. Fish. Mar. Serv. Res. Dev. Tech. Rep. 683: 13 p. (9)
684. REDDIN, D., AND D. E. WALDRON. 1976. 1975 Newfoundland and Labrador Atlantic salmon commercial catch data. Fish. Mar. Serv. Res. Dev. Tech. Rep. 684: 183 p. (9)
685. GRAINGER, E. H., AND J. E. LOVRITY. 1977. Biological oceanographic observations in the Eskimo Lakes, arctic Canada. Physical, nutrient and primary production data, 1961–1975. Fish. Mar. Serv. Res. Dev. Tech. Rep. 685: 108 p. (5)
686. METCALFE, C. D., M. J. DADSWELL, G. F. GILLIS, AND M. L. H. THOMAS. 1976. Physical, chemical and biological parameters of the Saint John River Estuary, New Brunswick, Canada. Fish. Mar. Serv. Res. Dev. Tech Rep. 686: 42 p. (6)

Rapports techniques

Les rapports techniques sont des documents de recherche qui revêtent une assez grande importance pour être conservés mais qui, pour une raison ou pour une autre, ne conviennent pas à une publication scientifique de fonds. Pour toute demande de renseignements concernant un rapport particulier, il faut s'adresser au service responsable.

Interpretive Articles Series

This new series commenced in 1966. The articles interpret work already published in primary journals. They appear at irregular intervals in various technical publications. Frequently an article essentially duplicates, condenses, or is based on an article in another series.

376. STRASDINE, G. A. 1975. Scientist support for the roe industry problems under continuous study. West. Fish. May. p. 61–63. (2)
377. SCOTT, K. R. 1976. 1,200 Baud telephone data transmission: Speeding up batch telemetry, part 1. Can. Control Instrum. October. p. 36–37. (4)
378. SCOTT, K. R. 1976. 1,200 Baud telephone data transmission: Speeding up batch telemetry, part 2. Can. Control Instrum. November. p. 22–24. (4)
379. UNESCO (working group 29 on monitoring in oceanography). 1973. Monitoring life in the ocean. UNESCO Tech. Pap. Mar. Sci. 15: 71 p. (1)
380. WALDICHUK, M. 1977. Control of marine pollution: An essay review. Ocean Dev. Int. Law J. 4: 269–296. (3)
381. WALDICHUK, M. 1977. Canada's proclaimed 200-mile fishing limit and environmental implications. Viewpoint 8(8): 175–184. (3)
382. WALDICHUK, M. 1976. Global marine pollution control and the new law of the sea, p. 33–50. *In* Seminar, implications to western north Atlantic countries of the new law of the sea, Bermuda, November 1976. Bermuda Biological Station for Research Spec. Publ. No. 14: 57 p. (3)
383. MANN, K. H. 1975. The impact of man on environmental systems in the maritimes. Proc. N.S. Inst. Sci. 27(Supplement 3): 43–46. (7)
384. SANDEMAN, E. J. 1974. Focus on fisheries, p. 101–110. *In* Proc. Can. Soc. Zool. Annu. Meet. Fredericton, N.B., 1974. (9)
385. WALDICHUK, M. (date unknown). Settleable organic wastes, p. 704–710. *In* Coastal zone management guidebook (Encyclopedia Section). (3)
386. WALDICHUK, M. (date unknown). Book review of R. J. Browning, 1974. Fisheries of the north Pacific. Alaska Northwest Publishing Co., Anchorage, 408 p. Pacific Search. (3)
387. WALDICHUK, M. 1975. Book review of J. H. Steele, 1974. The structure of marine ecosystems. Harvard University Press, Cambridge, 128 p. *In* Ocean Manage. 2: 345–360. (3)
388. WALDICHUK, M. 1975. Symp. rep: International symposium on discharge of sewage from sea outfalls. Ocean Manage. 2: 261–266. (3)
389. WALDICHUK, M. (date unknown). Book review: Gas bubble disease. D. H. Fickeisen and M. J. Schneider [ed.] Technical Information Center, Energy Research and Development Administration, Oak Ridge. 123 p. *In* Water Air Soil Pollut. 131–132. (3)
390. WALDICHUK, M. 1977. Book review: Tropical marine pollution. E. J. Ferguson Wood and R. E. Johannes [ed.] Elsevier Oceanographic Series 12, 1975, 192 p. *In* Ocean Manage. 3: 149–162. (3)
391. AYLES, G. B. (date unknown). Trout farming. Misc. Farm Entrep. 448–451. (4)

Articles explicatifs

Cette série a débuté en 1966. Les articles donnent une explication de travaux déjà publiés dans des revues prioritaires. Ils paraissent à intervalles irréguliers, dans diverses publications techniques. Souvent, un article se basera sur un écrit d'une autre série, le condensera ou le reproduira presque tel quel.

Translation Series

The following translations have been prepared by or for the Fisheries and Marine Service, for use in its investigations. Copies are available from Translation Services, Canada Institute for Scientific and Technical Information, National Research Council of Canada, Ottawa, Ontario K1A 0S2, at a cost of 22¢ per page and a minimum charge of $2.20. Information on translations can be obtained from the Scientific Information and Publications Branch.

HOMBERG, E. 1977. Gas-chromatographic separation of plant sterols. Fette Seifen Anstrichm. 79: 234–241. (Transl. from German by Fish. Mar. Serv. Transl. Ser. No. 4143, 1977)

PIROZHNIK, V. A. 1975. Composition and ratios of fatty acids in the subcutaneous fat of fur-bearing animals. Sb. Nauchno Tekhnol. Inf. Vses. Nauchno Issled. Inst. Okhot. Khoz. Zverovod. (47–48): 121–124. (Transl. from Russian by Fish. Mar. Serv. Transl. Ser. No. 4144, 1977)

OKUDA, Y. 1975. History of octupus processing and methods of processing. Sekai no ika tako shigen no kaihatsu to sono riyo Jpn. Mar. Resour. Res. Cent., Tokyo (5): 215–217. (Transl. from Japanese by Fish. Mar. Serv. Transl. Ser. No. 4145, 1977)

MIWA, S. 1975. State of squid and octopus use and processing. Progress report for the squid fishing survey in the world in 1974 (5): 185–213. (Transl. from Japanese by Fish. Mar. Serv. Transl. Ser. No. 4146, 1977)

ABE, K. 1977. Fish soy from Antarctic krill. Nyo Fudo Indasutori 19: 41–43. (Transl. from Japanese by Fish. Mar. Serv. Transl. Ser. No. 4147, 1977)

OGAWA, K. 1977. The role of bacterial floc as food for zooplankton in the sea. Nippon Suisan Gakkaishi 43: 395–407. (Transl. from Japanese by Fish. Mar. Serv. Transl. Ser. No. 4148, 1977)

BUDZYNSKA-TOPOLOWSKA, J. 1974. Fats and edible oils in rational human nutrition. Zywienie Czlowieka 1: 209–217. (Transl. from Polish by Fish. Mar. Serv. Transl. Ser. No. 4149, 1977)

LYUBAVINA, L. A., AND G. F. BAKANEVA. 1975. Changes in qualitative indices of veterinary fish oils of different transparency in storage. Tr. Polyarn. Nauchno Issled. Proektn. Inst. Morsk. Rybn. Khoz. Okeanogr. (36): 191–198. (Transl. from Russian by Fish. Mar. Serv. Transl. Ser. No. 4150, 1977)

Traductions

Les traductions dont il est question ci-après ont été préparées par ou pour le Service des pêches et des sciences de la mer, à des fins de recherche. On peut en obtenir des exemplaires, à 22¢ la page et à un prix minimum de $2.20 aux Services de traduction, Institut canadien de l'information scientifique et technologique, Conseil national de recherches du Canada, Ottawa (Ontario), K1A 0S2. La Direction de l'information et des publications scientifiques peut fournir des renseignements sur ces traductions.

List of Establishments

(1) Department of Fisheries and the Environment
Fisheries and Marine Service
Pacific Biological Station
P.O. Drawer 100
Nanaimo, British Columbia V9R 5K6

(2) Department of Fisheries and the Environment
Fisheries and Marine Service
Vancouver Laboratory
6640 N.W. Marine Drive
Vancouver, British Columbia V6T 1X2

(3) Department of Fisheries and the Environment
Fisheries and Marine Service
Pacific Environment Institute
4160 Marine Drive
West Vancouver, British Columbia V7V 1N6

(4) Department of Fisheries and the Environment
Fisheries and Marine Service
Freshwater Institute
501 University Crescent
Winnipeg, Manitoba R3T 2N6

(5) Department of Fisheries and the Environment
Fisheries and Marine Service
Arctic Biological Station
P.O. Box 400
Ste. Anne de Bellevue, Quebec H9X 3L6

(6) Department of Fisheries and the Environment
Fisheries and Marine Service
Biological Station
St. Andrews, New Brunswick E0G 2X0

(7) Department of Fisheries and the Environment
Fisheries and Marine Service
Marine Ecology Laboratory
Bedford Institute
P.O. Box 1006
Dartmouth, Nova Scotia B2Y 4A2

(8) Department of Fisheries and the Environment
Fisheries and Marine Service
Maritimes Regional Library
P.O. Box 550
Halifax, Nova Scotia B3J 2S7

(9) Department of Fisheries and the Environment
Fisheries and Marine Service
Research and Resource Services
Newfoundland Region
3 Water Street
St. John's, Newfoundland A1C 1A1

(10) Department of Fisheries and the Environment
Fisheries and Marine Service
Scientific Information and Publications Branch
Ottawa, Ontario K1A 0E6

(11) Department of Fisheries and the Environment
Fisheries and Marine Service
Canada Centre for Inland Waters
Great Lakes Biolimnology Laboratory
P.O. Box 5050
867 Lakeshore Rd.
Burlington, Ontario L7R 4A6

Liste d'établissements

(1) Ministère des Pêches et de l'Environnement
Service des pêches et de la mer
Station biologique du Pacifique
C.P. 100
Nanaïmo (Colombie-Britannique) V9R 5K6

(2) Ministère des Pêches et de l'Environnement
Service des pêches et de la mer
Laboratoire de Vancouver
6640 nord-ouest, prom. Marine
Vancouver (Colombie-Britannique) V6T 1X2

(3) Ministère des Pêches et de l'Environnement
Service des pêches et de la mer
Institut de l'environnement du Pacifique
4160, prom. Marine
Vancouver-Ouest (Colombie-Britannique)
V7V 1N6

(4) Ministère des Pêches et de l'Environnement
Service des pêches et de la mer
Institut des eaux douces
501, University Crescent
Winnipeg (Manitoba) R3T 2N6

(5) Ministère des Pêches et de l'Environnement
Service des pêches et de la mer
Station biologique de l'Arctique
C.P. 400
Saint-Anne-de-Bellevue (Québec) H9X 3L6

(6) Ministère des Pêches et de l'Environnement
Service des pêches et de la mer
Station biologique
St. Andrews (Nouveau-Brunswick) E0G 2X0

(7) Ministère des Pêches et de l'Environnement
Service des pêches et de la mer
Laboratoire d'écologie marine
Institut de Bedford C.P. 1006
Dartmouth (Nouvelle-Écosse) B2Y 4A2

(8) Ministère des Pêches et de l'Environnement
Service des pêches et de la mer
Bibliothèque de la région des maritimes
C.P. 550
Halifax (Nouvelle-Écosse) B3J 2S7

(9) Ministère des Pêches et de l'Environnement
Service des pêches et de la mer
Services des recherches et des ressources
Région de Terre Neuve
3, rue Water
St-Jean (Terre-Neuve) A1C 1A1

(10) Ministère des Pêches et de l'Environnement
Service des pêches et de la mer
Direction de l'information et des publications scientifiques
Ottawa (Ontario) K1A 0E6

(11) Ministère des Pêches et de l'Environnement
Service des pêches et de la mer
Centre canadien des eaux intérieures
Laboratoire de biolimnologie des Grands Lacs
C.P. 5050
867, ch. Lakeshore
Burlington (Ontario) L7R 4A6

ICLARM — a new international scientific center

The International Center for Living Aquatic Resources Management (ICLARM) is a new international, nonprofit, scientific center with the primary goal of assisting peoples of tropical and subtropical developing nations to develop and manage their aquatic resources to meet their nutritive, economic, and social needs. Incorporated in Manila in January 1977, ICLARM conducts and stimulates research on all phases of production, management, preservation, distribution, and utilization of fish and other aquatic organisms.

ICLARM will concentrate its initial efforts in Southeast Asia and the Southwest Pacific, and its principle programs will focus on critical problems in aquaculture, traditional fisheries, resource management and development, marine affairs, and education and training. In addition, ICLARM will undertake special projects on behalf of governments and regional and international agencies.

ICLARM's policies are determined by a Board of Trustees and executed under the direction of Director General John C. Marr. Advice on ICLARM's programs is provided by a Program Advisory Committee drawn from the international scientific community.

The core staff will be comprised of about 12 professionals with recognized expertise in aquaculture, nutrition, genetics, fish biology, population dynamics, economics, anthropology, civil engineering, and international law. Provision is also made for consultants, visiting scholars, and interns. Core programs and staff are funded by private foundations and governments.

Inquiries are invited from institutions wishing to propose cooperative programs, from interested donor institutions, and from potential visiting investigators and staff members. Direct correspondence to:

ICLARM
P.O. Box 1501 MCC
Makati, Metro Manila
PHILIPPINES

ICLARM — un organisme scientifique international nouveau

L'International Center for Living Aquatic Resources Management (ICLARM) est un organisme scientifique international nouveau, sans but lucratif, dont l'objectif principal est d'aider les nations tropicales et subtropicales à développer et gérer leurs ressources aquatiques de façon à subvenir à leurs besoins alimentaires, économiques et sociaux. Incorporé à Manille en janvier 1977, l'ICLARM effectue et encourage des recherches sur toutes les phases de la production, la gestion, la conservation, la distribution et l'utilisation des poissons et autres organismes aquatiques.

Au début, l'ICLARM concentrera ses efforts dans le Sud-Est asiatique et le Pacifique Sud-Occidental; ses principaux programmes seront centrés sur les problèmes critiques en aquiculture, pêches traditionnelles, gestion et expansion des ressources, questions maritimes, éducation et formation professionnelle. En outre, l'ICLARM se chargera de projets spéciaux pour le compte des gouvernements et des organismes régionaux et internationaux.

Un conseil d'administration définit les politiques de l'ICLARM qui sont ensuite exécutées sous la direction d'un directeur général, M. John C. Marr. Un comité consultatif des programmes, formé de membres de la communauté scientifique internationale, conseille l'ICLARM en matière de programmes.

Comme personnel, il y aura un noyau d'environ 12 professionnels possédant une compétence reconnue en aquiculture, nutrition, génétique, biologie des poissons, dynamique des populations, économique, anthropologie, génie civil et droit international. On pourra aussi faire appel à des consultants et recevoir des savants étrangers et des stagiaires. Des fondations privées et des gouvernements financent les programmes et le personnel centraux.

Les institutions désirant proposer des programmes coopératifs, les institutions donatrices intéressées, les chercheurs étrangers éventuels et les membres du personnel sont invités à soumettre leurs demandes de renseignements. On voudra bien adresser la correspondance à

ICLARM
P.O. Box 1501 MCC
Makati, Metro Manila
PHILIPPINES

Article Reprint Service

University Microfilms International, in cooperation with the *Journal of the Fisheries Research Board of Canada*, offers a highly convenient Article Reprint Service. Single articles or complete issues can now be obtained in hard copy. Articles cost $6 and $1 for each additional copy of the same article. Issues cost 10¢ per page with a $10 minimum order. Individuals who would like to know more about the Article Reprint Service should contact:

University Microfilms International
Article Reprint Service
300 North Zeeb Road
Ann Arbor, Michigan 48106, USA

Service de tirés à part

University Microfilms International, en coopération avec le *Journal de l'office des recherches sur les pêcheries du Canada*, offre un service très commode de tirés à part d'articles. On peut maintenant se procurer tirés à part sur papier d'articles séparés ou de numéros complets. Les tirés à part d'articles coûtent $6, plus $1 pour chaque copie supplémentaire d'un même article. Les numéros complets coûtent 10¢ la page avec minimum de $10. Pour plus de renseignements sur le service de tirés à part, on est prié de s'adresser à:

University Microfilms International
Article Reprint Service
300 North Zeeb Road
Ann Arbor, Michigan 48106, USA

Publications diverses spéciales

L'Homme, les lacs et la prolifération des algues

J. R. VALLENTYNE

(1978, 196 p., N° de catalogue Fs 4-31/22F; Canada $3.75, autres pays $4.50)

Cet ouvrage, préparé à l'intention des non-spécialistes, traite des lacs et de la façon dont ils sont affectés par les apports de matières nutritives découlant des activités humaines (eutrophisation due à l'Homme). Alors que le thème central de l'ouvrage porte sur le phosphore en tant que clé de la lutte contre l'eutrophisation due à l'Homme, une analyse des causes réelles fait ressortir la nécessité de limiter la croissance démophorique. Le lecteur trouvera en fin de volume un glossaire des termes scientifiques, des références suivies d'une liste de lectures supplémentaires ainsi qu'un appendice comprenant un bilan de la situation en 1974 et une série de tableaux et de figures.

Guide pratique de l'anatomie et de la physiologie du saumon du Pacifique

L. S. SMITH ET G. R. BELL

(1978, 15 p., N° de catalogue Fs 4-31/27F; Canada $2.50, autres pays $3.00)

La présente publication, illustrée de dessins et de photographies, contient une description de l'anatomie macroscopique des saumons du Pacifique. Les aspects de l'anatomie et de la physiologie qui présentent un intérêt particulier pour les biologistes des pêches y sont soulignés. De plus, le système cardio-vasculaire est étudié en détail à l'aide d'angiogrammes et de pièces moulées en plastique rigide du système sanguin. On ne discute que brièvement de l'anatomie du squelette, des muscles et du système nerveux. Notons que presque toute cette information s'applique également au saumon atlantique et aux truites.

Procédés de traitement et de conservation du maquereau. Étude et bibliographie annotée.

J. R. DINGLE

(1978, 69 p., N° de catalogue Fs 4-31/30F; Canada $3.00, autres pays $3.60)

La présente publication rassemble la documentation technique et scientifique parue avant 1974 et ayant trait au maquereau dans l'alimentation humaine. Il comprend 184 résumés ainsi qu'une liste de sujets choisis.

Ces publications sont en vente à

Imprimerie et Édition
Approvisionnements et Services Canada
Ottawa K1A 0S9

Les chèques ou mandats-postes, payables à l'avance en monnaie canadienne, doivent être faits à l'ordre du Receveur général du Canada.

Journal of the Fisheries Research Board of Canada

Journal de l'Office des recherches sur les pêcheries du Canada

JFRBAK35(3)279–380(1978)
ISSN 0015-296X

Volume 35, No. 3, March 1978

Volume 35, n° 3, mars 1978

A simple fish-population model including environmental influence, for two western Atlantic shelf stocks — **R. H. Loucks and W. H. Sutcliffe Jr.** 279–285

Sorption of arsenic and cadmium and their effects on growth, micronutrient utilization, and photosynthetic pigment composition of *Asterionella formosa* — **H. L. Conway** 286–294

Buoyancy response to changes in water velocity and its function in creek chub (Semotilus atromaculatus) — **G. Berezay and J. H. Gee** 295–299

Applicability of phosphorus budget models to small Precambrian lakes, Algonquin Park, Ontario — **W. A. Scheider** 300–304

Concentrations of nutrients and chlorophyll on a cross-channel transect in Juan de Fuca Strait, British Columbia — **A. G. Lewis** 305–314

Concentrations and kinetics of phosphorus fractions in water from streams entering Lake Memphremagog — **R. H. Peters** 315–328

Notes

Feeding response of Atlantic salmon (*Salmo salar*) alevins in flowing and still water — **D. M. Rimmer and G. Power** 329–332

Comparison of two methods used by divers for sampling benthic invertebrates in deep rivers — **C. F. Rabeni and K. E. Gibbs** 332–336

Outplant method for phenological studies of *Chondrus crispus* in mechanically harvested beds — **L. A. Hanic and J. D. Pringle** 336–338

Survey of trace metal contents of suspended matter in the St. Lawrence estuary and Saguenay fjord — **D. Cossa and S. A. Poulet** 338–345

Anesthetic and handling stress on survival and cortisol concentration in yearling chinook salmon (*Oncorhynchus tshawytscha*) — **R. J. Strange and C. B. Schreck** 345–349

Perspectives

Facing the long term: an inquiry into opportunities to improve the climate for research with reference to limnology in Canada — **J. R. Vallentyne** 350–369

Obituary — Otto Christian Young — **N. M. Carter** 370–371

Book Reviews/Comptes rendus: Ichthyology (K. F. Lagler, J. E. Bardach, R. R. Miller, and D. R. M. Passino) **P. H. Cahn**; Biological monitoring of water and effluent quality (Edited by J. Cairns Jr., K. L. Dickson, and G. F. Westlake) **R. McV. Clarke**; Impact of acid precipitation on forest and freshwater ecosystems in Norway. Research Report 6/76 (Edited by F. H. Braekke) **R. J. Beamish** 372–374

Books received/Livres reçus 374
Coming next month/À paraître le mois prochain 375
Recent publications/Récentes publications 376–379
Announcements/Avis 380

© Minister of Supply and Services Canada 1978
Ministre des Approvisionnements et Services Canada 1978